LIFE OF PLANTS

KEEBLE

CLARENDON SCIENCE SERIES

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Oxford University Press
London Edinburgh Glasgow Copenhagen
New York Toronto Melbourne Cape Town
Bombay Calcutta Madras Shanghai
Humphrey Milford Publisher to the UNIVERSITY

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Acer platanoides, showing one year's growth.

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LIFE OF PLANTS

BY

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211877
30.4.27

OXFORD
AT THE CLARENDON PRESS
1926

Printed in England
At the Oxford University Press
By John Johnson
Printer to the University

PREFACE

THE growth of Science is like that of a tree. From seed-sowing to harvest the time is long and tedious to those who look for fruits. But during that time there go on obscurely and below as well as above ground unending successions of very wonderful developments. Not until they have been accomplished are blossom and fruit produced, and then profusion and beauty are apparent for all to see. Yet to those who tend them the science and the tree are beautiful always, alike in their obscure beginnings and in their brilliant fulfilment. To show this has been my object: to suggest that Science is more than a body of doctrine—an illumination of life. I have not succeeded, for the task has proved beyond my powers. Nevertheless those who know how hard the task is will be most lenient in their judgement; for they know also that it is important for the welfare of mankind that such attempts to impart understanding of the method and to convey impressions of the beauty of Science should be made again and again until at last they do perchance succeed. Although of my part I can only say 'What is writ is writ'—'would it were worthier', of that of my colleagues, Mr. Wilkins and Mr. Kempin, I speak with

warm and grateful appreciation. To the former are due the drawings from which the larger number of the illustrations are reproduced, and to the latter the photographs.

I am also deeply indebted to the Editor of the Series, Mr. Julian Huxley, for close, acute, and friendly criticism of the pages as they passed through the press.

F. K.

The School of Botany,
The University,
Oxford.

CONTENTS

PAGE

I. *Introductory*.—The part which plants play in the world. Plants of high and low degree : unicellular and multicellular. The flowering plant. The origin of land vegetation. Plankton and benthos. The garden of the world 1

II. The Vegetable Kingdom and the members thereof. Green and non-green plants (Fungi and Bacteria). The wheat grain : composition : germination. The wheat harvest of the world 20

III. The manufacture of food-materials by the green plant. The raw materials : mineral salts, water, and carbon dioxide. Absorption of water and mineral salts by the root. Water- and sand-cultures. The source of nitrogen to the ordinary green plant and to leguminous plants. Root-nodules and nitrogen fixation. Absorption of carbon dioxide by the green leaf. The root, stem, and leaf in relation to the work of assembling raw materials 44

IV. The absorption of radiant energy by the green leaf. Chloroplasts and leucoplasts. The chlorophyll-containing tissues : palisade and spongy parenchyma. Chemical and physical properties of chlorophyll. Photosynthesis of carbohydrates : and the synthesis of organic nitrogen-compounds. Nitrifying bacteria 68

V. The mobilization of food-materials. Physical and chemical properties of carbohydrates and proteins. Diffusion. Osmosis : osmotic pressure. Colloids and non-colloids : the colloidal state. Enzymes and the part they play in mobilization. The conducting system of the root and stem 91

PAGE

VI. The use of the food-materials for construction and power-production. Growth and differentiation of cells and tissues. Respiration. Aerobic and anaerobic life. Fermentation and decay. Self-supporting (Autotrophic) and non-self-supporting (Heterotrophic) flowering plants: Saprophytes, Parasites, Semi-parasites. Symbiosis. Insectivorous plants 131

VII. The environment of the land plant: water-supply and sunlight. Stomata as regulators of gaseous exchange. The mechanism of stomatal movement. The role of transpiration in the economy of the plant. The transpiration stream (ascent of sap) 160

VIII. Variation and Heredity: Evolution. Reproduction: asexual and sexual. Cell and nuclear division: the Chromosomes as the material bases of Heredity. The experimental breeding of plants. Mendelian inheritance. 188

IX. The plant commonwealth and its government; the integration of the plant. The Sensitive Plant (*Mimosa pudica*); stimulus and excitation; receptors and effectors; the transmission of excitation; chemical messengers (hormones) 225

INDEX 251

LIST OF ILLUSTRATIONS

FIG.		PAGE
	Acer platanoides, showing one year's growth .	*Frontispiece*
1.	Stages in the development of buds of horse-chestnut . .	7
2.	Scale leaves from bud of horse chestnut	9
3.	A species of Chlamydomonas, a unicellular green plant, and a species of Euglena, a unicellular animal . . .	11
4.	*Fucus platycarpus*, a brown seaweed of benthic habit .	15
5.	Yeast: budding and spore-formation	24
6.	*Agaricus campestris*, the common mushroom . . .	26
7.	Spore-formation in the mushroom	27
8.	The structure of the wheat grain	32
9.	Effect of potassium nitrate on the growth of seedlings .	34
10.	Starch grains from endosperm of barley	37
11.	Seedlings, illustrating the behaviour of cotyledons in germination	39
12.	Water-cultures of maize	49
13.	Root nodules of the pea	53
14.	Root-hair, enlarged and diagrammatic	57
15.	Apparatus for demonstrating continuous absorption of carbon dioxide by illuminated green leaves . . .	60
16.	Surface view of epidermis of cherry laurel, showing stomata	64
17.	Transverse section of the leaf of the beech . . .	71
18.	The dependence of starch formation on illumination and supply of carbon dioxide	78
19.	Record of the rate of diffusion of potash in solution . .	99
20.	Osmotic apparatus	101
21.	Stages in development of a plant cell	103
22.	Diagram of plasmolysed cells of the lower epidermis of a leaf of *Tradescantia discolor*	105
23.	Transverse section of the young stem of a Dicotyledon, the sunflower	117
24 A.	Transverse section of the young root of a Dicotyledon (buttercup)	118
24 B.	Part of Fig. 24 A more highly magnified, showing central cylinder	119
25 A.	Transverse section of a Monocotyledon (maize) . .	120
25 B.	Transverse section of one of the vascular bundles shown in Fig. 25 A	121

FIG.		PAGE
26.	Transverse section of phloem of *Cucurbita Pepo*, showing sieve-plates	122
27.	Sieve-tubes of *Cucurbita Pepo* in longitudinal section.	122
28.	Transverse section of part of the stem of the sunflower	123
29.	Transverse section of the stem of the lime	126
30.	Transverse section of part of the stem of the lime in its fourth year	127
31.	Longitudinal section of wood of sunflower	129
32.	Cells of the endosperm of the castor-oil plant	133
33.	Longitudinal section through root-tip of maize	135
34.	*Nepenthes Ratcliffiana*. Photograph by Malby	155
35.	Broom-rape, parasitic on clover	156
36.	Dodder, parasitic on the common tansy	157
37.	Guard-cells of a stoma	165
38.	Porometer	171
39.	Potometer	175
40.	Xerophytic plants naturalized in the Riviera	183
41.	Sexual reproduction of Chlamydomonas	191
42.	Flower of *Cypripedium Leeanum*	195
43.	*Magnolia Watsoni*. Photograph by Malby	197
44 A and B.	Diagrams illustrating (A) the structure of the pistil, and (B) the process of fertilization	199
45 and 46.	Semi-diagrammatic representation of nuclear division. Mitosis (below) and meiosis (above) in *Allium* sp.	205
47.	Diagram of mitosis and meiosis	209
48.	Inheritance of palm- and fern-leaf character in the Chinese primula	217
49.	Sensitive plant (*Mimosa pudica*), showing the leaves in the normal position and after stimulation	229
50.	Seedlings of the grass *Phalaris canariensis* submitted to phototropic stimulation	231
51.	Response of root of broad bean to geotropic stimulus	235

I

INTRODUCTORY

The part which plants play in the world. Plants of high and low degree : unicellular and multicellular. The flowering plant. The origin of land vegetation. Plankton and benthos. The garden of the world.

THE study of plants is an adventure into another world the inhabitants of which are strangely different from those of the animal world. Members of the world of plants feed without mouths, move without limbs, 'see' without eyes, and find their way in and about the world without the aid of brain or nervous system.

In the exploration of the earth and the settlement of the land plants are the pioneers and animals but camp-followers. The plant world is a world of pioneers. Its members prepare the way, and only after plants have occupied a land may animals possess it. Plants not only colonize tracts of new land but also make them fertile. Even on the barren face of a limestone cliff the grey and yellow lichens gain a hold, penetrate the surface of the rock, and help the forces of Nature, rain and running water, frost and snow and wind, to disintegrate it and create from the rock the mineral debris which is the beginning of soil. Not until many generations of some of the simpler and less exacting plants have colonized the soil and have lived and died thereon is it rendered fertile enough to support higher kinds of vegetation. Soil fertility is a memorial of plant activity. The fertility of the earth, created by plants, is also maintained by them. A soil from which all vegetation was banished would in course of time

pass back into the sterile state in which it was before its advent.

Plants are the universal food-providers; they—or rather some of them, and, in particular, green plants—possess the power of manufacturing the food-materials on which their own nourishment and that of the animal world depend. The process of manufacture, of which man has discovered so many important details that he is now able to some extent to imitate it, involves, like all manufacture, the use of raw materials and a source of power. The food-materials which the green plant manufactures are chiefly of two kinds, sugars and proteins: the former composed of the three elements carbon, oxygen, and hydrogen, and the latter composed of these, together with nitrogen and other elements. The raw materials used by the green plant in the manufacture of sugar are water and carbon dioxide—simple substances abounding on the earth. The energy utilized is the radiant energy of the sun. In the process of manufacture the raw materials disappear, and so does the energy. But neither the elements of which the raw materials are composed nor the energy are lost or destroyed. They abide in the manufactured food substances until, in course of time, one or other of these substances, for example sugar, uniting with oxygen, undergoes combustion, when the original raw materials from which it was formed are reproduced and the energy locked up or potential in the sugar is liberated. In this manner the manufactured food-materials provide the energy used by living beings. Not only, as George Stephenson said, does the sun drive the steam-engine; it likewise drives the living engines —plant and animal.

As for the steam-engine: the story of the source of its energy is briefly this:—The sun shone in far-off times on the leaves of prehistoric green plants which grew, it may be, by estuarine waters. Of the radiant energy which fell on a leaf, some was absorbed by the green tissues and served for the manufacture of sugars. Much of the sugar was consumed by

the plant in the course of its life, but some, undergoing relatively little chemical change, became part of the woody skeleton. Presently the tree died and fell into muddy ooze. Before decay could complete its work of destruction the plant was embalmed and carbon and hydrogen and oxygen, united originally by the sun's energy and the plant's activity, remained united still, though as time went on some of the hydrogen and oxygen was lost and the plant-remains became more and more carbonized. Therein the energy derived from the sun remained dormant until in the furnace of the steam-engine the coal unites with oxygen, re-forms water and carbon dioxide, and liberates the long-stored energy: and so in the singing of the escaping steam there is an echo of the incidence of a ray of sunlight on a green leaf ages before the beginning of recorded time.

The study of plant nutrition discloses also the facts, surprising to any one who is used to contemplate the differences between plants and animals, that the materials used by plants in the construction of their tissues are of the same kinds as those used by animals, and that the power employed by both animal and plant worlds in the work of living is derived from the same ultimate source. The green plant is an accumulator of energy. Each molecule of sugar or other food-material which it makes may be likened to a storage battery of such efficiency that only when the molecule is decomposed is the store of energy liberated. So lavish is the manufacture by green plants exposed to sunlight that the products suffice not only to form the fabric of their own bodies and those of animals but also to supply energy for both worlds.

It might seem impossible to add to this recital of the obligations of the animal to the plant world; but recent discoveries have shown that it is by no means complete. Beside the food-materials supplied by plants which serve the animal for body-building and as sources of energy, there are others of more obscure nature which play the part of natural preventive medicines. If they are present in the food of

animals bodily health is maintained ; but if they are absent from it malnutrition and disordered growth result. These accessory food bodies or vitamines are, at all events in the main, plant products, though curiously enough it is not yet known what, if any, is the part they play in regulating the growth of plants themselves.

The fact that fresh vegetables are conducive to health has long been known. It is recorded that Nelson, when he kept the sea with the Grand Fleet watching the French ports year after year, maintained the health of his seamen by exercise and onions ; and it is a matter of history that Captain Cook discovered during his voyages the value of fresh vegetables in preventing scurvy. From hints such as these, science, by isolating and testing the materials contained in plant tissues, has discovered a new class of food substances which behave as regulators of bodily growth and health ; and in so doing has shown that the dietary debt of animals to plants is greater than was previously supposed.

Plants constitute the Ministry of Health of the world. They are also its Sanitary Authority. By the ordered activities of successions of plants of simple organization dead remains of things which once lived are decomposed stage by stage until they are resolved into the simple inorganic substances wherefrom green plants constructed them.

The burden of universal food production borne by the world of green plants has left its mark indelibly on the bodies of every individual belonging to that world. For, as mechanism made by man reveals in plan and detail of construction the purpose for which it is designed and the manner whereby it fulfils its purpose, so does living mechanism. Each organ of the plant and animal body has, as it were, engraved in its tissues the function that it has been called into existence to discharge ; and the more specialized the organ, that is, the more it is dedicated exclusively to work of one kind, the more its plan and details of construction are indicative of its function.

The division of labour which is the mark of all higher organisms is accompanied by and based on an adaptive differentiation of the body. For example, the thin green sheets of tissue which are called leaves (see *Frontispiece*) show by their disposition and delicacy and by their structure that to them is confided as a prime function the task of absorbing and utilizing the radiant energy of the sun. The scales which enclose the buds of flowering plants are also leaves of like origin with, and of construction essentially similar to, that of foliage leaves; but, as indicated by their position, shape, and texture, their function is the more mechanical though none the less important one of affording protection to the frail tissues of the bud (Fig. 1). In the hard dryness or the varnish-like covering of their surfaces, their diminished size, and in the curiously opportune habit of dying and falling off just when the foliage of the bud begins to unfold may be seen evidence of the specialized function of bud-scales.

Comparative study of buds and bud-scales of common trees and shrubs as they appear at different times of the year is worth making, not only as an exercise in observation, but also because it throws light on the nature of the almost endless diversity presented by plants. All flowering plants are built on a common plan. Each is composed of a very limited number of members—root or descending axis with lateral roots, shoot or ascending axis with lateral branches and leaves, and reproductive organs borne by the flower.

As is illustrated by comparison of the buds and bud-scales of different kinds of plants, not a little of the diversity among plants is brought about by old members undertaking new functions. So far-reaching may be the change of appearance that a member charged with this or that special function may cease to look like what it is. In such cases the member in question may only be shown to belong to this or that category —root, stem, leaf, &c.—by tracing its origin and course of development, or by comparing the plant, member by member, with more normal and closely allied plants.

In the case of some shrubs and trees, e.g. dogwood (*Cornus sanguinea*) and wayfaring tree (*Viburnum Lantana*), the buds have no specialized scale-leaves. They are naked and the progressively smaller leaves which arise in due order from the rudimentary axis of the bud and cover its growing-point are all of one kind. When spring comes and the bud unfolds, none of the small leaves falls off. All persist and grow into foliage leaves. Each develops a leaf-stalk and becomes large and green, and as the axis of the bud elongates at the same time to form a branch each pair of leaves, borne on somewhat swollen nodes of the stem, becomes separated from the succeeding pair by a longer or shorter joint or internode of the stem.

In the majority of shrubs and trees, however, the buds are enclosed by bud-scales and in all of them the bud-scales, no matter how rudimentary and unleaf-like they are, may be shown to be of leaf-like nature, that is, morphologically equivalent to leaves. Bud-scale and foliage leaf alike arise each as a superficial lateral outgrowth of the axis or young stem of a bud ; each is of limited growth and not like a stem which may exhibit unlimited growth, increasing in length and thickness year after year. The order in which successive bud-scales are borne is identical with that of the foliage leaves which precede and succeed them. For example, in the horse-chestnut (*Aesculus hippocastanum*) the foliage leaves are in opposite pairs with successive pairs alternating with one another, and so also are the brown varnished scale-leaves of the buds (Fig. 1) ; in the plum and many other plants a line joining the point of attachment of the successive foliage leaves to the stem forms a spiral, and so also are the bud-scales spirally disposed on the miniature axis of the bud.

Although the morphological equivalent of leaves, bud-scales are rarely complete leaves. A fully developed foliage leaf may be seen to consist of blade (lamina), stalk (petiole), and leaf-base (see *Frontispiece*) which sometimes, as in roses and violets, &c., bears leaf-like outgrowths termed stipules.

FIG. 1. Stages in the development of the buds of horse-chestnut (*Aesculus hippocastanum*). 1, buds in resting stage; 2, unfolding; 3, fully opened.

In some few plants, lilac (*Syringa vulgaris*), and privet (*Ligustrum vulgare*), each bud-scale consists of a leaf of which only the blade is developed. Yet, although the petiole is suppressed, it may be caused to appear. If, in spring, when the buds begin to break, the young inner leaves of a privet or lilac bud are removed, growth of the scale-leaves is resumed, and in the absence of their younger rivals they develop into normal, stalked, green foliage leaves. More frequently, as in the horse-chestnut, maple (*Acer campestre*), sycamore (*Acer pseudo-platanus*), and flowering currant (*Ribes sanguineum*), the bud-scale is the morphological equivalent of the leaf-base—that part of the normal foliage leaf which attaches the leaf-stalk to the stem. In these cases suppression of blade and stalk is attended by excessive growth of the leaf-base. In any of these plants, but particularly in the flowering currant, sycamore, and horse-chestnut, transitions may be seen as the bud opens (Fig. 2). They show bud-scales, some consisting of leaf-base only, others of leaf-base with a rudimentary blade, and yet others half-way between scale- and foliage leaves in which all three parts of the leaf may be distinguished. In the alder (*Alnus glutinosa*), beech (*Fagus sylvatica*), and oak (*Quercus robur*), it is the stipules only which are represented in the scale-leaves. In some of the bud-scales of the alder a lamina may develop and thereby reveal the morphological nature of the bud-scale, but in the beech and oak the bud-scales develop no farther, and it requires the application of comparative methods to determine that they are nothing but leaves reduced to stipules.

Inasmuch as organized mechanism exhibits adaptation to its function, it is to be expected that the green plant will show throughout its plan and details of construction no less than in its mode of life, signs of adaptation to its work of food production ; and if that be so, its general structure must be very different from that of animals which are discharged by Nature from the obligation of sharing in that work. Of these signs the most impressive, after greenness, is the

immobility of the plant world. Animals must seek their food and tend therefore to be rovers. Plants—at all events those that form the dominant vegetation of the land—must win the ingredients of theirs from earth and air and sun, and are therefore stay-at-homes. Although the immobility is more apparent than real, nevertheless the general run of green plants is fixed and stationary, each rooted in its narrow plot.

FIG. 2. Scale-leaves from a bud of the horse-chestnut, showing transitions from leaf-base only to leaf-base with lamina—petiole suppressed.

Thus firmly established, the plant may explore the earth and atmosphere and reach up towards the sun. In the earth the roots seek and find not too precarious stores of water and mineral substances. In the atmosphere the least movement of the air brings to the leaves new supplies of carbon dioxide ; and by reaching upwards towards heaven the stem may outdistance competitors for light. Because some raw materials come to it from below and others, as well as radiant energy, from above, the fixed green plant is two-ended. It extends by growth in both directions and makes the best of both

worlds. It is perhaps conceivable that green plants might have secured supplies of raw materials by entirely different means, without surrendering power of moving about and without becoming half-subterranean and half-aerial beings. It is not impossible that distant ages may see a plant world composed of individuals of appearance and habit altogether different from those of the present day, a world which has succeeded in solving the problem of food-manufacture by novel methods better than those which are now in vogue among plants. If so, the descendants of our trees and shrubs and herbs, instead of dominating the world, may be ousted from their predominant position, and either pass away altogether or survive here and there, limited in number and restricted in range, occupying only the poorer regions which the new types of vegetation—at present only evoked in the imagination—may leave uncultivated.

Though not inconceivable, the advent of this new world of plants is not likely; for, since the remotest times in which there are fossil records of vegetable life, all the many different kinds of land plant which have lived upon the earth and have passed beyond the lowest stages of development have been characterized by the same essentials of habit and organization as those manifest to-day in the green plants of forest and field. They have all been fixed organisms and have all developed the two-endedness which men are so accustomed to see that they do not marvel at it. So constant is the adherence of land plants of all epochs and of very different stages of development to this plan of construction that the suggestion has been made that two-endedness was already a fixed character of the plant world before members of that world existed on the land at all.

According to this suggestion plant life began in the sea. There it passed through the earliest stages of its evolution, acquired green pigment, and developed forms of many different kinds, all minute and of relatively simple organization, and all alike in the enjoyment of the freedom of the seas. They were free to swim or float wherever light drew them or

the current bore them. In this marine, free or plankton stage, green plants, of microscopic size, possessed no roots to anchor them permanently to the ground, but floated passively buoyed up by the waters, or propelled themselves by motile extensions of their bodies. Plants which may be survivors of this stage still live in the sea and also in fresh water. One of them (see Fig. 3 A) illustrates the relative simplicity of this type of organism and the difference between plankton and land plants. Invisible to the naked eye and so small that a thousand might lie easily side by side on a line one-eighth of an inch long, each individual shows nevertheless, when examined by means of the microscope, a definite and elaborate structure. The oval body which constitutes the cell or protoplast is composed of living substance, cytoplasm, in part of which (the chloroplast) green pigment, chlorophyll, identical with that of higher green plants, is contained. A denser, specialized mass of living substance, the nucleus, is to be seen in the clear, upper, flask-shaped part of the cytoplasm. The body terminates in a minute cytoplasmic knob from which project two slender, living threads—the flagella—by the rhythmic movement of which it is propelled through the water. On one side of the body is a small spot of pigment—the eye-spot—which helps the organism to register the direction in which light falls upon it and thereby to move toward the light.

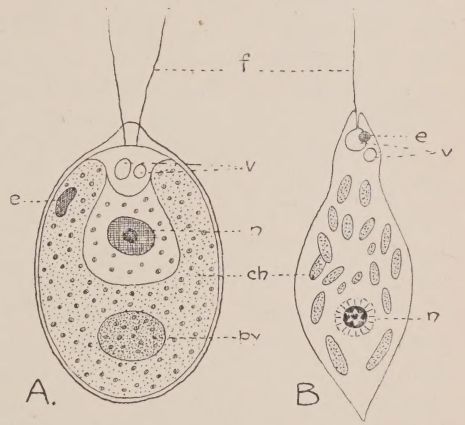


FIG. 3. A, a species of Chlamydomonas—a unicellular green plant; B, a species of Euglena—a unicellular animal. *ch*, chloroplast; *n*, nucleus; *e*, eye-spot; *f*, flagellum; *v*, vacuole; *py* (in A), pyrenoid (a mass of protein of uncertain function).

At the moment of its birth this organism may have no visible covering, but its nakedness is almost immediately covered by the formation from the surface layer of cytoplasm of a membrane of non-living substance—a cell-wall which, though thin, is continuous and hence serves as a barrier across which no solid particles may pass. Through it only water and materials dissolved therein may be absorbed.

Although the plants of the primitive plankton were doubtless, like those now found in the surface waters of the sea, of varied structure, this organism, a species of the genus Chlamydomonas (coated monads), serves to illustrate the kind of beings they were. Active, freely moving, possessed of a rudimentary 'sense organ', this single-celled organism seems strangely different from the higher members of the world of land plants. Yet it may have been not distantly related to their remote ancestors. Its green pigment and continuous solid coat or cell-wall are characters which Chlamydomonas shares with other and even the most highly organized plants.

It is probable that in the earliest phases of the primeval plankton-period the world of life showed no distinction into plant and animal kingdoms, and that it was only in later phases of the period that organisms arose with distinctive animal characteristics. Even Chlamydomonas, so plant-like in the possession of chlorophyll and in the complete investiture of its body by a coat of cell-wall substance, may pass through phases in which it assumes animal-like characteristics. It may settle on organic debris, withdraw its flagella, round itself off into a sphere, and lose its chlorophyll. In this stage it may increase by growth and division of its body, obtaining, after the fashion of an animal, the material for growth from organic substances. In a similar way, simply organized aquatic forms of life of animal nature may show upon occasion plant-like characters. For example, one of the common, microscopic, unicellular organisms which exists to-day (*Euglena sp.*, Fig. 3 B) possesses the distinctly animal characteristic that the investiture of its body

stops at and does not cover a short tract or gullet, which leads from the surface into the body. The existence of the open passage permits of the entry of solid particles which, if of food-yielding kind, undergo digestion and serve for the nourishment of the animal. This mode of nutrition is characteristic of the animal world; to sweep solid substances into a digestive tract and there to extract from them and to absorb into the body such nourishment as these solids may yield. In sharp contrast with this mode of nutrition is that of the plant world. The continuous solid coat or wall which invests the plant-body admits of the passage of no solid particles. Only substances in solution may pass across the wall and reach the protoplasm, that is, the cytoplasm, nucleus, and all other living parts of the cell.

The animal obtains its ready-made food-materials from without in solid or liquid form. The green plant, though it uses essentially the same food-materials, makes them within its body from solutions of raw materials which it obtains from soil and air. When these opposed characteristics became fixed, the one in one set of organisms, the other in another set, the dividing line between animal and plant world was established and henceforth the members of the two kingdoms pursued their several and divergent ways.

Yet, in spite of their animal attributes, species of Euglena contain pigment identical with the chlorophyll of green plants, and like green plants make use of it in the manufacture of food-materials.

There is no reason to doubt but that during the later plankton-phase the seas contained both plant and animal organisms. If it did the wastage of life must have been great indeed. The physical conditions of plankton life are severe enough for frail, minute, and ephemeral things. Rough seas and tides and untoward currents take a heavy toll: for to be borne below the depth to which the sun's rays penetrate spells darkness and death. To these must be added the no less formidable risks of incorporation and digestion within the

bodies of the animals of the plankton. Yet in spite of ever-recurring wastage the plant plankton maintained itself and assumed diverse forms of which some have left descendants which survive in the seas to-day.

For how long the primitive world of life consisted only of plankton cannot even be guessed; but in view of the multiplicity of forms which were evolved, and of the slowness as measured by years with which evolution seems to progress, it was probably very long. Nevertheless in course of time the plant world developed a new kind of organism. Some of the plankton plants acquired a new habit of life. True to their role of pioneers, primitive plankton adventurers gave up their freedom and became fixed organisms or benthos. Settling on the shelving shores of shallow seas, the forerunners of the higher plants threw out anchor-like projections from their bodies and by these holdfasts grappled themselves to the rocks or anchored in the ooze. The world of plants was now divided into two sub-kingdoms: plankton, which remained free, and benthos, fixed and immobile. With the latter lay the future. They developed their two-endedness. The lower root-end became a strong holdfast, the free end grew out to form a thallus consisting of threads, or plates, or masses of tissue composed of many cells. It even in some cases became differentiated into an axis bearing lateral extensions—first crude foreshadowings of stem and leaf, which later on were to become fixed and standardized in the higher forms of vegetation. So the bodies of plants of the benthic phase, fixed by their holdfast root-ends, floated in the sea after the fashion of seaweeds (Fig. 4), which indeed may perhaps be their much-changed descendants.

The phase during which plankton and benthos divided the marine plant world between them, like the plankton-phase which preceded it, may have endured for ages, lasting until the land surfaces of the earth became hospitable to plants. When that happened the casual but sure hand of chance could scarcely fail to lead some benthic plants to land. For

FIG. 4. *Fucus platycarpus*, a brown seaweed of benthic habit. Thallus consisting of *d*, holdfast; *st*, stalk; *m*, midrib with (*f*) foliose expansions; *s*, swollen ends of branches; *c*, conceptacles containing male and female reproductive organs.

as the crust of a pie may show during baking local rises and falls, so the crust of the earth has undergone like movements. As a sea-coast rose the plants fringing it would find themselves emerging from the water, and if the process were sufficiently slow and gradual some might survive in brackish shallow waters, and even resist the desiccation to which they risked exposure at low tides. Now and again throughout those ages benthic plants had a chance of becoming land-colonists; and although in most cases they no doubt failed, here and again some, perchance succeeding, became the forerunners of the present-day vegetation of the earth. If so, the members of the Vegetable Kingdom which gained a foothold and endured and underwent transformation into higher forms were already committed by age-long habit acquired in the sea to a fixed state and a two-ended form.

That state and form gave them their opportunity, but also prescribed their limitations, so that, in spite of the almost infinite variety of form which land plants exhibit, and in spite of the diversity of conditions which obtain on the earth, none of the higher land plants has been able to throw off the shackles of the past. They all remain fixed and two-ended. They also all remain aquatic to this extent, that only in ground where the soil particles are covered with films of water can their roots live.

To regard the land plant solely as an exquisitely adjusted mechanism for doing its work of living is wrong: for to do so is to ignore the past and to ignore the past is to misread the present. The story of the evolution of the land plant would rather seem to be that of living mechanism which, having arisen in relation to one set of conditions—those of the sea-marge—found itself translated into a very different set of conditions—those of the dry land. Its past the plant carried with it as a help and as a hindrance. The holdfast root helped, the power to grow towards the light helped: nevertheless the fixed habit and two-ended form imposed limitations on the ways which, had the past been

different, the green plant of the sea might have employed to solve the problems of terrestrial existence.

The problems were not easy of solution. The difficulties which confronted the first plant migrants from the sea were great and numerous, and no less great and no fewer are the difficulties which have attended their every advance toward the complete colonization of the land. The extent to which plants now possess the earth, and the variety of form which they have assumed in fitting themselves to diverse stations, may be taken as measures of the success with which they have overcome these difficulties. Few indeed are the regions that have resisted their advance. In favoured parts of the world with sufficient rainfall plants of the dominant form of vegetation have become trees and make the woodlands of the world. In less favoured regions grassland replaces woodland, and, except where man intervenes, these two great formations maintain themselves unchanged. Though seeds of other kinds of plants are sown there by the lavish hand of chance, the trees and lesser plants in occupation of natural woodland persist generation after generation, and it is but rarely that an invader gains a permanent foothold among them. So it is with grassland. In the natural state the plants native to it maintain year after year a high degree of constancy of kind and number.

These formations—woodland and grassland—are closed formations—closed because they are already full and because their possessors are so nicely adjusted to the conditions which obtain there that if any plot of ground falls vacant the claim of possession is paramount. Thus it is that the vegetation of the world now enjoys a great orderliness. As surely as the spring, and with it, the bluebells appear in the woods and the primrose blooms on woodland banks. Yet earlier in the year the dark green leaves and pale yellow flowers of the dog mercury (*Mercurialis perennis*) may be seen above the dead brown leaves which litter the outskirts of beech woods ; and onward throughout the year, in punctual regular succession,

the plants of woodland and grassland, of hedgerow and ditch-side, of moorland and marshland, proclaim at the time of their flowering their permanent possession each of its special tract of land and time within the year.

As in an ordered and established garden every plant has and keeps its place, so in a large and general way is it in Nature's garden. When that garden—the world—was first laid out it was open to all plant-comers. It offered sites of great variety. Some well-watered and warm, veritable plant paradises, became like tropical jungles so densely occupied as to be wellnigh impenetrable. Those plants which came to be at home there, in specializing to make the best of hot and moist stations, so lost the power of resisting cold that none of them can live now in our climate without the shelter of a glass-house. They, the macrotherms, plants with lives attuned to high temperatures, stand in sharp contrast with the mesotherms of temperate regions and the microtherms which flourish only at temperatures so low as to mean death to other plants. Other sites, though of lesser warmth, still sufficed for tree growth and hence for woodland vegetation. Yet others, with a more precarious water-supply, served well enough for grasses and herbaceous plants which can fit their active life into the favourable season and die down and rest in the adverse season of the year. In these situations the competition of plant with plant was fierce and continuous and not all the competitors survived.

But all the time the wind and birds and other animals and flowing water were one way or another carrying seeds and scattering them broadcast over the earth. And so a plant which failed to meet the competition in woodland or in grass-land might still chance on land outside and might make good there. In this way the less hospitable regions of the earth came also to possess each a vegetation of its own, till even the dry and wind-swept moorland had its gorse, the bleak mountain-side its purple ling and heather, the sand dunes by the sea their yellow horned poppies and the marram grass

which binds the shifting sand. The ponds and streams gave asylum to land plants which therein found a faint echo of their maritime origin and became once more aquatic. Even the sea-shore between tide-marks gave harbourage, and flowering plants like the grass wrack (*Zostera marina*), foiled on dry land, became once again benthos. The boglands provided a home for Sphagnum moss, the insect-catching butterwort (*Pinguicula vulgaris*) with its white or mauve violet flowers, and the sundew (*Drosera rotundifolia*). Until the only regions open freely to new-comers are the desert lands—the hot, rainless, sandy wastes of tropical and semi-tropical countries, the desert of snow and ice around the poles, and the mountain peaks far above the snow-line. These are still open. They and new land arising from the sea are the only regions left for plants to conquer.

II

The Vegetable Kingdom and the members thereof. Green and non-green plants (Fungi and Bacteria). The wheat grain: composition: germination. The wheat harvest of the world.

In the natural world, in spite of the apparent subservience of plants, men and animals are held in thrall by them. Men and animals depend on plants for food, and food-supplies regulate and determine the increase and migrations of animal and human societies. As society grows more complex, so the demands made by mankind on the world of plants increase. That world feeds and clothes mankind. It supplies the power employed alike in the animal body and in industrial enterprise, and the amount of consumption of such plant-products as coal and timber serves as a sure index of the state of industrial development of a country. Even though, forgoing recourse to the plant world, man resorts to water power and transforms the energy of rivers and waterfalls into electrical energy, he nevertheless must still apply to plants for rubber and gutta-percha to insulate the cables which carry the current and for oils to lubricate the machinery.

The progress of chemical discovery has, however, already begun to work a change in the relation between animal and plant worlds, and to encourage expectation that in years to come the animal world will be freed from the gentle bondage in which it is now held by the plant world, and that mankind, by using natural forces, inorganic substances, and chemical knowledge, may be able to supply his needs for raw materials and power without the manufacturing agency of plants. Already the chemist has succeeded in building up sugars from inorganic materials, and has gone far towards synthesizing the yet more complex nitrogen-containing proteins which are essential constituents of protoplasm.

Although his efforts to produce proteins synthetically have not yet been crowned with complete success, the chemist has nevertheless contrived means for speeding up the protein-synthesizing activity of plants. Before this achievement supplies of the inorganic nitrogen compounds used by plants in the building up of proteins were limited to those which the vegetable kingdom itself produces. Chief among them are nitrates which owe their presence in fertile soil to the activities of certain kinds of micro-organism (see p. 89). But the rate of production of nitrates by soil bacteria is not always rapid, and wastage of soil nitrates, so far as the land is concerned, goes on often at a great pace. Winter rains leach out the soluble nitrates of the soil so rapidly that even fertile ground may contain at any one moment no more than enough nitrate to supply the needs of a single crop. To make good the recurrent loss farmers have long been accustomed to apply to the land nitrogen-containing artificial manures, nitrate of soda from the saltpetre beds of Chile, or sulphate of ammonia obtained as a by-product in the manufacture of coal-gas. Even so, the growth of the world's crops is limited by insufficiency of cheap supplies of nitrogenous manures. Now, by the use of electrical power the chemist is able to augment on a vast scale the natural supplies by bringing nitrogen of the air into combination with other elements, and producing nitrates, salts of ammonia, urea, &c., which, when supplied to the soil, enable crops to obtain all the nitrogen which they can use.

In other directions also the chemist is gradually ousting the plant from its place of world's manufacturer. Synthetic dyes, indigo and other, compete with those extracted from plants, and every year sees the announcement of the discovery of new synthetic products. Nevertheless, in spite of these wonderful performances in applied chemistry and the promise of discoveries yet more wonderful, the plant world still remains, and will long remain, the great source of supply of materials and energy for the sustenance of the lives of animals

and men, and for the maintenance and development of the social and industrial life of mankind. The tortoise of fabulous cosmogony, on whose back stands the elephant supporting Atlas who bears the world, is still sustained by the grass of green fields.

In this work present and past activity are laid under contribution. By their present activity plants provide the world with an almost innumerable variety of commodities. By their past activities they have made the world's fuels—peat, coal, and perhaps petroleum—the first, a legacy from not so long ago and still accruing, the others bequeathed long before man the beneficiary appeared upon the earth to claim them.

All the divisions of the Vegetable Kingdom take part in the payment in kind ; but it is the members of the highest and lowest groups that make the most lavish contributions.

The seed-bearing plants (*Spermaphyta*), which include both coniferous and ordinary flowering plants, supply food-stuffs, fibres and timbers, resin and rubber and gutta-percha, camphor, waxes and varnishes, unguents, spices and condiments, perfumes and poisons and dyes and drugs. These plants sustain the life of the earth. The Algae, members of the lowest division (*Thallophyta*), support the teeming life of the seas ; in the plants of plankton and benthos marine life has its sustenance.

The plants belonging to the intermediate divisions of the Vegetable Kingdom, the ferns and their allies (*Pteridophyta*) and the mosses and liverworts (*Bryophyta*), make at the present day a lesser contribution to the world, though testimony to the past contribution of plants having affinities with present *Pteridophyta* is borne by every smoking chimney in the world. They were coal producers. Even the mosses—gregarious, slender, and curiously constructed—yield tribute in the form of peat. Though relatively unimportant economically, the ferns and mosses are of great scientific importance, for study of them helps to point the way along which the evolution of plants has progressed.

The lowest of the divisions (*Thallophyta*) comprises not only the Algae (see Fig. 4) but also the Fungi (cf. Figs. 5 and 6). Alga and fungus, although allied, differ profoundly in their modes of life. The one contains chlorophyll and is self-supporting, the other, lacking chlorophyll, lacks also the power to feed itself. The food requirements of fungi are, however, similar to those of other organisms, plant or animal; hence fungi must, after the fashion of animals, obtain food-supplies from outside sources. A fungus therefore lives perforce either as a parasite, preying on other plants, or as a saprophyte, battening on the dead remains of once living things.

In this respect fungi resemble the members of yet another division of the Plant Kingdom—the Bacteria (*Schizophyta*)—which, however, are generally of such minuteness, and always of such extreme simplicity of visible structure, that their exact status in the world of life, whether primitives or degenerates or a miscellaneous collection of diverse origin, none may define. Like the fungi, bacteria in general lack chlorophyll, and like them, with certain astonishing exceptions (see p. 89), they live as saprophytes or parasites.

This underworld of plants—the fungi and bacteria—plays so great a part in the world's work that it deserves a brief description.

Imagine the single protoplast which constitutes the body of Chlamydomonas (Fig. 3 A) much reduced in size, so that even under the highest power of the microscope it looks small, its chloroplast and eye-spot gone, nucleus scarcely distinguishable, flagella persisting or lost, wall not of cellulose but of a protein-like or gelatinous substance, shape either remaining spherical or modified in one of many different ways—to become rod- or comma-like, &c.—and a rough picture of the body of one of the simpler bacteria forms itself in the mind. Sometimes the cell units remain associated, enclosed in a common mucilaginous envelope so that as they increase in numbers they form a bacterial colony visible to the naked

eye. Reproduction is effected by division, whereby from one cell two are produced, each of which grows and divides so that the rate of increase is often extremely rapid. When food-supplies are exhausted the cells, ceasing activity, may give rise each to a thick-coated, dry, minute spore which in many cases is resistant to extremes of temperature and to drought. In this state a bacterium rests; its previously active life becomes latent until borne by air or water it comes at last to some spot in which active life may be begun again.

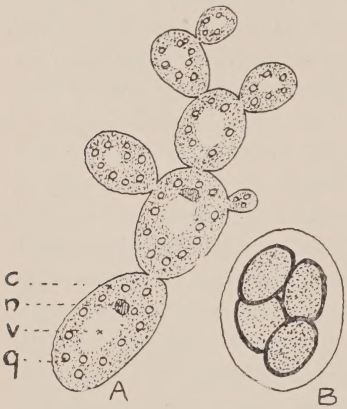


FIG. 5. Yeast (*Saccharomyces cerevisiae*). A, budding; B, forming spores. *c*, cytoplasm; *n*, nucleus; *v*, vacuole; *q*, oil globules.

To picture some of the various forms presented by fungi imagine that Chlamydomonas, whilst retaining cytoplasm and nucleus, loses chloroplast, eye-spot, and flagella, and there is a model of a yeast-cell (Fig. 5). The cell grows actively, undergoes division so that a new cell at first smaller than the original appears like a bud attached to it. The daughter-cell may in turn bud off a cell, and when this occurs a chain of yeast-cells is produced. Hence, at one time the yeast plant may appear as a unicellular organism, and at another, having formed a chain of cells, it is multicellular.

Like bacteria, yeasts may produce spores. The protoplasmic contents of a cell undergo division and form from four to eight cells, each surrounded by a wall of its own (Fig. 5 B). The spores, liberated by the disruption of the wall of the original cell, may undergo desiccation without injury. Thus dormant, they are carried by air currents in vast numbers and sown throughout the world, so that

some surely fall on 'good ground' and spring up and multiply.

Or, to picture an individual belonging to one of the other groups of the simpler fungi, imagine Chlamydomonas having lost its chloroplast, flagella, and eye-spot to grow out as a long, fine, tubular, branched or unbranched thread or hypha, its cytoplasm forming a thin layer against the inside of the cell-wall and tending to accumulate at the tip of the hypha: the nucleus dividing as the cell grows so that at intervals along the microscopic, tubular body a nucleus lies embedded in cytoplasm.

To convert this picture into one of a fungus of a higher group it only needs to interpose cross-walls between the successive nuclei of the hypha. Thus among higher fungi the plant body may be truly multicellular, and inasmuch as both types of structure presented by fungi have their counterparts among algae it is possible that the different classes of fungi have evolved each and independently from algal ancestors.

In most fungi spore-formation takes place. Those that live on land produce, often in vast numbers, small, round or oval, coated spores, destined to be borne by air currents; but those that live in water give rise to naked, motile spores which bear flagella and may possess an eye-spot in witness of their algal origin.

Besides bearing spores, some of the lower fungi propagate their kind by a process of sexual reproduction (see Chap. VIII). In this process two cells specially formed for the purpose of reproduction fuse with one another to produce one cell which is the starting-point of a new individual. Others, for example many of the higher fungi, have lost the power of sexual reproduction, so that the group is of great interest as illustrating evolution by loss or reduction—lost chloroplast and with it lost power of self-support, lost eye-spot and flagella (which, however, reappear in the motile spores of lower fungi), and lost power of sexual reproduction. Yet though in structure

the fungi are degenerate, in fending for themselves and finding some secure niche—some special plot in which to live—they are at no loss. Judged by their form they are degenerate, but judged by their powers of getting on they are no less efficient than the green plant itself, and it may be safely predicted that fungi and bacteria will flourish

FIG. 6. *Agaricus campestris*, the common mushroom.

in the world to its benefit and detriment so long as green plants go on doing their work of universal food-provision.

In the higher fungi—toadstools, mushrooms, &c.—the vegetative body is composed of large numbers of branched hyphae which form the cobweb-like *mycelium* or spawn which runs through the ground or in living or decaying wood, &c. When ripe for spore-production the hyphae, growing rapidly, intertwine and give rise to a massive spore-bearing structure, the sporophore, which pushes up from the substratum into

the air and constitutes the toadstool or mushroom (Fig. 6). On some part or other of the sporophore spores arise in countless numbers, and generally in groups of four, but in some varieties of cultivated mushrooms in groups of two (Fig. 7). Each spore, when set free, if it fall on suitable ground germinates and gives rise to a new plant.

As the rain falls upon the just and upon the unjust, so falls the invisible, wellnigh unceasing rain of air-borne micro-

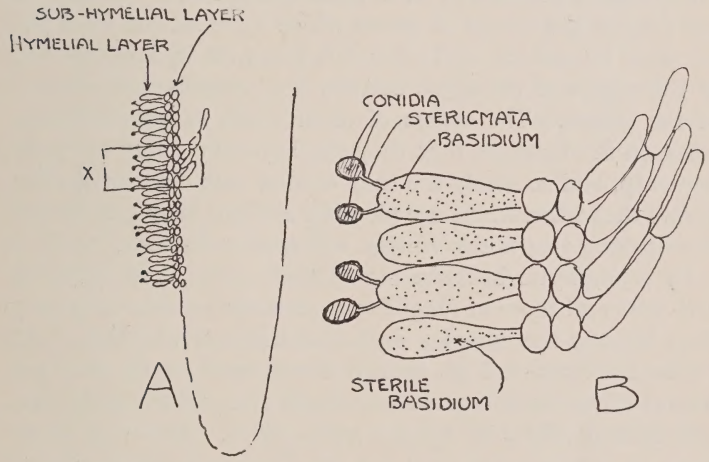


FIG. 7. Spore-formation in the mushroom. A, section through a gill showing the position of the spores (conidia); B, part of A enlarged to show detail.

organisms of different kinds. Few fall on good ground; yet so great are their powers of increase that, year in, year out, the many known species of micro-organisms survive, and there is no case on record of any one kind having disappeared from off the face of the earth.

The ubiquity of micro-organisms is also shown by the fact that organic matter of almost any kind if exposed to the air not only undergoes decay, but each kind always undergoes much the same sort of decay. Milk turns sour, apples become bitter, jam and old leather become mouldy, and butter rancid:

facts which testify to the sureness and punctuality with which each micro-organism reaches its evolutionally appointed place and the regularity and precision with which it carries out the chemical changes in which it is a specialist. A piece of moist bread exposed to the air forms almost invariably a seed-bed in which air-borne spores of one or other of certain moulds sow themselves, germinate, and give rise to a bluish grey or white felt-work, which, spreading, soon produces a crop of spores. Every apple which falls in a cider orchard bears with it to the ground the spores of yeasts which have settled from the air upon its surface, and after decay has set in fermentation of the sugars of the apple betrays the presence and activity of the yeasts. The spores of other kinds of yeasts are so common in vineyards that they are borne by every marauding wasp, and so surely are they carried that the vine-grower knows that when wasps are plentiful and are busy puncturing the ripening grapes the vintage will readily ferment.

Of saprophytic bacteria many kinds occur, and by their activities and those of fungi decay proceeds in ordered stages. Step by step the complex organic substances of which dead bodies are composed are broken down, until finally they are resolved into the inorganic substances from which they were constructed originally by the green plant. Thus: a green plant absorbs nitrates from the soil; by the synthetic power of the plant the nitrogen contained therein is combined with other elements and becomes a constituent of a protein: as such it is incorporated with the living substance of the plant: presently the plant dies; relays of micro-organisms destroy stage by stage its chemical components, including the proteins the nitrogen of which is liberated in inorganic form, for example, as a constituent of ammonia: the ammonia serves to support the life of the nitrifying bacteria of the soil: by their action it is oxidized, and nitrates are produced: so the wheel of nitrogen-change comes full circle, and nitrogen is once again in a form fit to be borne on its eventful and never-ending journey through the kingdom of living things.

Other bacteria grow only in living tissues. They are parasitic specialists. Each by its growth and activity brings about changes in the body which it infects, and the changes may be so pronounced that pathologists are able to infer from the symptoms the presence of the pathogene in the blood or tissues of the patient, and to prove the truth of the inference by isolating and cultivating the micro-organism outside the body. In rapidly increasing numbers of diseases of this kind research has shown how the poisons (toxins) produced by pathogenic micro-organisms may be neutralized or destroyed, and the disease prevented or cured.

Although most kinds of pathogenic bacteria attack animals, some have specialized as plant parasites. Conversely, among fungi are found many kinds which are parasitic on plants, and relatively few which attack animals. Any one who notices the rusty yellow spots or streaks on wheat or rose or hollyhock, or the black patches common on badly-grown tomatoes, may observe an example of parasitism due to a fungus. The point of a needle thrust first into the soft black spot on a diseased tomato and then into a sound tomato fruit, serves to transplant sufficient of the mycelium of the pathogenic fungus to communicate the disease to the sound fruit, on which in due course appears a black spot of constantly increasing size.

From this rapid and rough survey of the Vegetable Kingdom, it is at least clear that varied and unceasing activity reigns there. Behind the impassive mask which vegetation wears, great and diverse work of manufacture is on foot. How great and how diverse it is may be learned by tracing the life-history of the green plant from the beginning to the end.

Among green plants wheat holds a predominant place, and therefore it is fit that it should serve to illustrate the theme. The seed-like fruit or grain of wheat contains—as do seeds in general—much dry matter and relatively little water. Whereas water makes up from three-quarters to nine-tenths or more

of the weight of leaves, tubers, and fleshy fruits, it constitutes little more than one-tenth of the grain of wheat or other cereal (see Table I).

TABLE I

PERCENTAGE COMPOSITION AND FOOD VALUE OF WHEAT GRAIN AND OTHER VEGETABLE PRODUCE

	Water.	*Protein.*	*Fat.*	*Carbo-hydrates. Starch and Sugar.*	*Fibre.*	*Ash.*	*Calories per lb.*
Wheat Grain	10·6	12·2	1·7	71·3	2·4	1·8	1625
Potatoes .	78·3	2·2	0·1	18·4	0·4	1·0	375
Beet . .	87·5	1·6*	0·1	8·8	0·9	1·1	200
Cabbage .	89·6	1·8*	0·4	5·8	1·1	1·3	165
Cucumber .	95·9	0·8*	0·1	2·1	0·5	0·4	70

* Percentage of proteins and other nitrogen-containing substances.

So long as they remain dry, seeds lie dormant—alive, but inactive. The state of ' suspended animation ' may endure for a long time, but if unduly prolonged the power of resuming active life gradually wanes. Some kinds of seed (onion, parsnip, &c.) lose power of germination in the course of two or three years : others retain it for many. Certain leguminous seeds kept with no particular care have been shown to be capable of germination after nearly one hundred years, and it is possible that—buried in undisturbed soil—the seeds of such plants as charlock and foxglove may lie dormant for even longer periods. Wheat grains possess fair powers of endurance and may germinate after thirty or forty years, but the recurrent announcement of the germination of mummy wheat—that is, wheat from mummy cases thousands of years old—has no support except in the credulity of mankind.

When soaked in water or put in moist earth a grain of wheat from a recent harvest soon begins to germinate. The speed with which germination takes place depends in part on the age of the grain, and in part on the kind of harvest in

which it was gathered. If the grain has been kept for more than three or four years it germinates slowly and capriciously, but if it be of a good and recent harvest the seeds germinate readily and simultaneously. The rate of germination depends also on external conditions. Only between certain temperatures does wheat or other seed germinate at all. In the case of wheat the lower limit is about 2° C. and the upper limit about 50° C. Germination depends also upon access of air to the soil. Sown in water-logged soil the germination of wheat is slow and may fail altogether. That oxygen is the constituent of air necessary for germination may be shown by observing the behaviour of submerged grains. For this purpose, barley, which germinates readily under water, is better than wheat. Submerged in ordinary tap-water it germinates and puts forth green leaves, but if tap-water is boiled thoroughly for a long time so as to drive off its dissolved oxygen, and cooled in such conditions that but little oxygen is reabsorbed, germination of grains of barley submerged in it is extremely slow, and may be suppressed altogether if the water is prevented from absorbing oxygen from the air by a covering layer of oil.

In order to follow the course of germination wheat grains may be placed in a saucer lined with clean, white blotting-paper, moistened and kept moist with water, and covered with another saucer similarly lined. The grains swell as they absorb water, and become plump, and in the course of a few days the first visible sign of germination is seen in the emergence of the roots. The number of the first or seminal roots is three in wheat and rye, and five in barley and oats. They force their way out, rending the covering tissue as an eager finger may tear a threadbare glove. The seminal roots arise from the lower part of the small, somewhat lozenge-shaped, whitish embryo (Fig. 8), which lies near the surface close to one end of the grain. The upper part of the embryo, still confined within the grain, consists of a short, squat stem or shoot axis. Its apex is enclosed by a succession of leaf-

rudiments which arise from the axis close to one another, and are smaller and smaller the nearer they are to the growing-point. The leaves wrap round the bare, dome-shaped apex or growing-point of the axis, and constitute a bud similar in all respects to that borne on the stem of an adult plant. One other peculiar part of the embryo is known as the scutellum

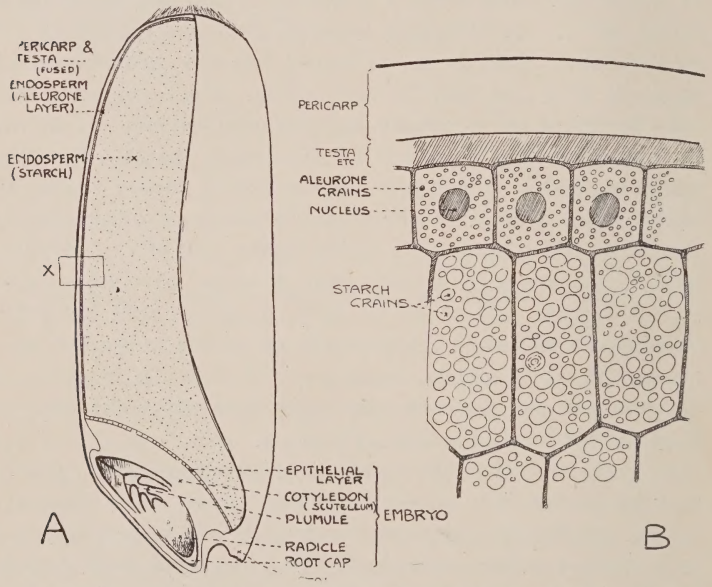


FIG. 8. A, longitudinal section of a grain of wheat (*Triticum sativum*); B, section (more highly magnified) showing the aleurone grain layer and starch-containing cells of the endosperm.

(Fig. 8). It looks like neither leaf, stem, nor root. This organ consists of a shield-shaped outgrowth from the axis of the embryo, and its superficial (epithelial) layer makes contact with the tissues which lie outside the embryo. The scutellum, which is large and conspicuous in the germinating grain, withers away as soon as germination is complete. It may therefore be regarded as an embryonic organ—that is, one which, whilst it fulfils some important function in early

life, is useless to the adult individual. The morphological nature of the shield-like structure is uncertain, but there is some ground for regarding it as a modified seed-leaf or cotyledon. In support of this view it may be pointed out that wheat belongs to that subdivision of flowering plants (Monocotyledons) the members of which are characterized by the possession of a single seed-leaf. In this respect, as in many other respects, Monocotyledons stand in sharp contrast with the other subdivision of flowering plants, the Dicotyledons, which almost invariably bear two cotyledons (cf. Fig. 11, p. 39). Moreover, the embryos of not a few Monocotyledons —onion, &c.—possess a curious, somewhat shield-shaped or cup-like sucker, which serves a purpose similar to that of the scutellum, and is manifestly formed from the tip of the cotyledon.

Not until the seminal roots have reached a certain length is there any other clear sign of life in the germinating grain. It is a matter of life and death for the root to get itself established firmly in the soil, so that it may be in a position not only to provide mechanical support to the seedling but also to obtain water and other nutriment. Unless the roots become wedged tightly in the soil the later emergence of the leaves is rendered difficult, and, what is worse, the rocking of the young plant in the soil interferes with both the growth of the roots and their work of absorption. This, indeed, is true of mature as well as of seedling plants, and the gardener who neglects to stake plants is the nurseryman's best friend; for he is bound to lose them and will need to buy more.

Inspection of Table I suggests the nature of the materials which the young roots require. The delicate leaves which the plant must presently push forth are composed of about nine-tenths of water, and water in continuous supply the plant must have. Of carbohydrates and proteins there is a liberal store in the grain, but of mineral matter (see *Ash*, Table I) the store is very meagre. It would therefore seem probable that the early and rapid growth of the seedling roots is due not merely

to their position in the embryo and to the need for providing the seedling with a fixed point of support, but also to the imperative necessity of acquiring mineral substances from the soil. An experiment made with seeds of mustard and of cress confirms this conclusion (see Fig. 9). If a few seeds of either or both kinds be sown on coarse muslin stretched and fixed over the mouth of a glass jar nearly filled with water they will

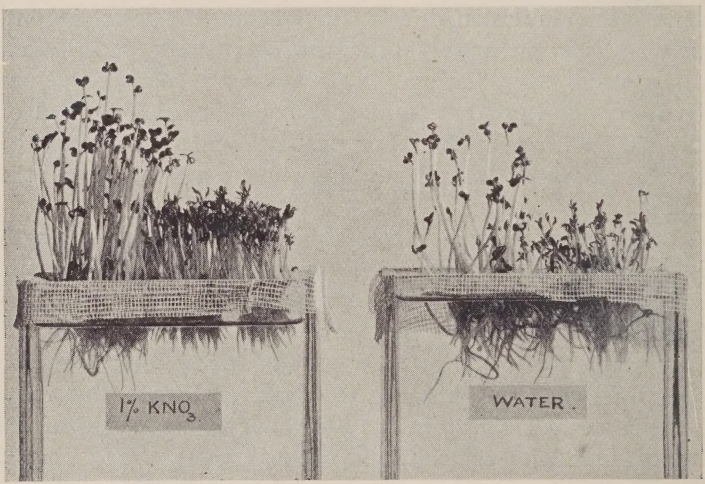


FIG. 9. Effect of potassium nitrate on the growth of seedlings. Mustard and cress sown simultaneously in a 1 % potassium nitrate solution and in water.

germinate and in time grow into healthy seedlings ; but if so much nitrate of soda as will go on the tip of a blade of a pocket-knife be added to the water, the growth of the aerial parts of seedlings is much more vigorous, though, as shown in the illustration, that of the roots is less (cf. p. 178). Like most plants in Nature, seedlings are hungry for nitrogen, and the addition of a very small quantity of a soluble and suitable compound of nitrogen is a great help to their development.

Shortly after the roots have emerged and grown in length the first leaf pushes out like a spear-head from the upper part

of the wheat embryo. If the saucer covering the grains fits so closely as to exclude light the first leaf is not green, as it would be if exposed to light. It is etiolated—that is, white or yellowish, very long and flabby. In the absence of light the aerial parts of plants (stem and leaf) exhibit disordered growth. Not only does chlorophyll fail to develop, at all events in the general run of plants, but the relations between the leaf and the stem are altered. This is seen even better if, instead of wheat grains, seeds of mustard or some other dicotylous plant are germinated. In absence of light the leaves remain small, and the stem, which in plants grown in the light is short and stocky, elongates excessively, becoming long, thin, and so weedy that it can scarcely stand upright. These facts are of more significance than would at first appear, for they show that besides playing a part in the manufacturing processes of the green plant light exercises a regulatory effect on plant growth. As children deprived of sunlight suffer from disordered growth, so do seedlings, and as sunlight is necessary for the perfect health of human adults, so is it for the health of mature green plants.

The next stage in germination of the wheat grain is a curious one. A new group of roots destined to replace the seminal roots pushes out from the base of the stem. This replacement is peculiar to the cereals and other Monocotyledons, and does not generally occur in dicotylous plants. The embryos of Dicotyledons, as a rule, possess a tap-root which, after emerging from the seed, gives rise to lateral roots. Laterals borne on the main or tap-root may be described as true roots, and roots which arise from the base of the stem, as adventitious roots. It is true that, as may be seen when a cutting strikes root, Dicotyledons are also capable of producing adventitious roots, but as a rule the seedling Dicotyledon bears a true root which generally persists and forms the root system of the adult plant; whereas, even if a Monocotyledon embryo bear a main root, it soon aborts and is replaced by adventitious roots.

The first leaf of the wheat seedling is rudimentary. It

consists almost entirely of a sheathing leaf-base, and so does the second, which, rolled on itself, presently protrudes through the cylindrically rolled base of the first. If the seedling be kept continuously in darkness this may be as far as it gets. Growth wanes, development ceases, and after lingering for a while the seedling dies. On the other hand seedlings exposed to light grow green and vigorous. In either case germination is accompanied by changes in the part of the grain which lies outside the embryo. Originally hard and flinty, and still firm after the grain has absorbed water, this tissue, known as the endosperm (Fig. 8), becomes more and more soft and watery as germination proceeds, until finally little of it is left. In the intact grain, the thin-walled cells of which the endosperm is composed (Fig. 8 B) are for the most part full of starch grains, each of which appears under the microscope as a solid, oval body consisting of lighter and darker concentric layers. The outermost layer of the endosperm, known as the aleurone layer, contains not starch but protein grains. The two, starch and protein, may be distinguished by the fact that when stained with iodine starch takes on a blue, and protein a yellow-brown colour. In the grain beginning to waste by germination the scutellum may be seen to have become much enlarged, and the close relations between it and the endosperm are such as to suggest that the scutellum plays an important part in the transference of food-materials from endosperm to embryo. This in turn would help to explain both the transitoriness and curious form of this embryonic organ.

Examination of the contents of the endosperm at successive stages of germination shows the nature of the wastage that goes on in the contents of its cells. Protein grains disappear, starch grains swell, lose their marked stratification, become riven with fissures, cease to give a good blue colour with iodine, until finally only pale ghostly outlines of the grains remain (see Fig. 10). Simultaneously with the disappearance of protein and starch from the endosperm, these substances make their appearance in the seedling. Hence it can scarcely

be doubted but that food-materials are conveyed in some way from endosperm to the young plant. If so it is clear that what is food for animals is also food for plants. For the miller makes flour from wheat endosperm. In the process of

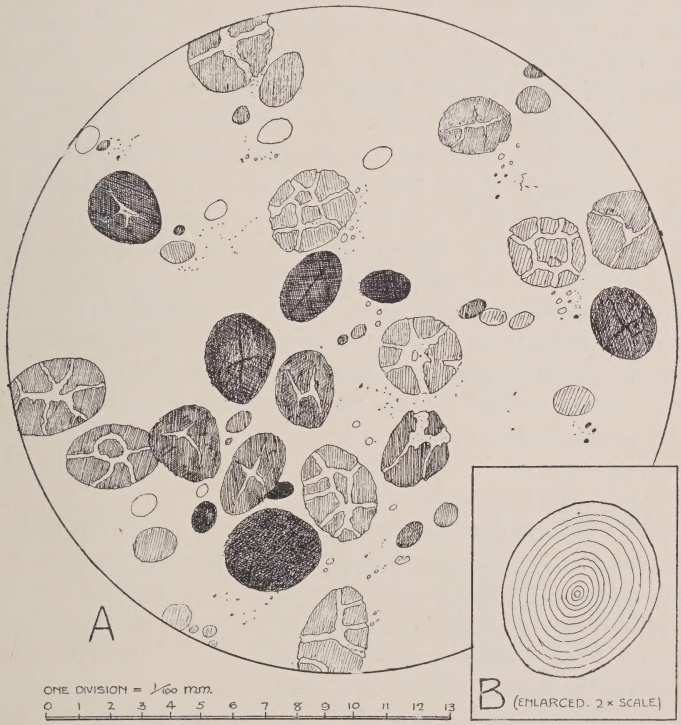


FIG. 10. Starch grains from endosperm of barley. A, grains disintegrating under the action of diastase; B, intact grain showing striation.

milling he discards husk and embryo. Despite the fact that they contain substances of great nutritive value to human beings, these parts are not contained in ordinary white flour but are sold as ' offal ' for animal feeding.

That the embryo obtains food-materials from the endosperm may be shown by experiment. If, after the grain has begun

to germinate, the bulk of the endosperm be removed, the seedling, even though exposed to the light, remains puny for a long time. A similar experiment may also be made, and more easily, with one of the large-seeded, leguminous plants. In such a plant the ripe seed has no endosperm but rich reserves of proteins and carbohydrates are contained in the two large cotyledons which, borne opposite one another on either side of the base of the young stem (plumule), make up the major part of the seed. In some plants of this kind (broad bean) the cotyledons never emerge from the seed-coat, but in others they are withdrawn from it by the growth of the young stem and, becoming green and borne up into the air, reveal by their appearance and structure the fact that they are indeed leaves (cf. Fig. 11). If from a germinating seed, broad bean, runner bean, wheat or mustard, the cotyledons or endosperm, as the case may be, are removed as soon as germination has begun, the seedling which emerges looks like a dwarf beside one which has been left intact. Later, when it has developed other leaves, the seedling which was deprived of its food-supplies may recover, but for the time being its growth is crippled.

These observations and experiments raise many interesting questions: how are starch and proteins transferred from the endosperm (or from the cotyledons) to the seedling? what happens when these supplies are exhausted? what becomes of the food-materials, and in what way do they serve to nourish the plant? These are some of the questions which must be answered if success is to attend our inquiry into the life of the plant, but the wheat plant itself, growing rapidly to maturity, has a prior claim and they must wait until a later chapter.

The young wheat plant free from the shrivelled grain, with roots firmly fixed in the soil and green leaves growing upward towards the light, keeps for a long time yet its stem just beneath the surface of the ground. The shoot-axis remains short and squat, but becomes much stouter than it was in

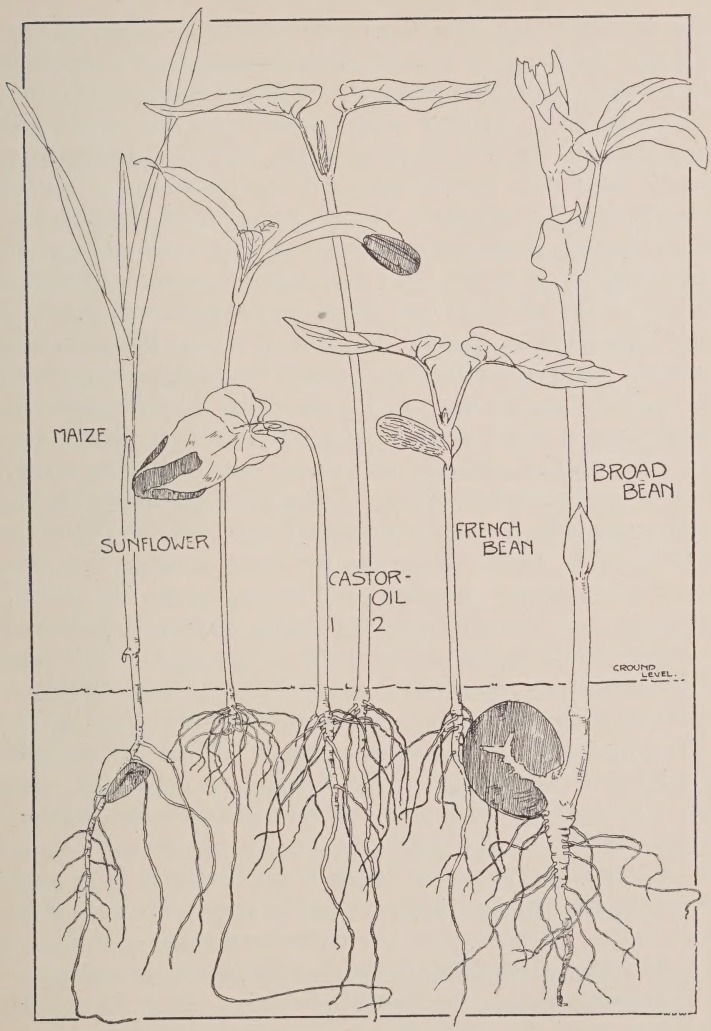


FIG. 11. Seedlings, illustrating the behaviour of cotyledons in germination.

the seedling stage, and one by one it sends leaves up into the air. In the axils of some of the leaves arise lateral buds in all respects like the terminal bud of the embryo, and they also grow and send forth a succession of leaves. The plant has tillered. It is now approaching maturity and getting ready for flower production. Although no sign is visible above ground, the axes or stems of the wheat plant ripe to flower have in the meantime been organizing each a miniature inflorescence on which the rudimentary flowers are formed. When all is ready and conditions are favourable the axes of each inflorescence elongate rapidly, and soon the flowering shoots are waving in the field. This is the shooting of the ear. When fully mature each of the numerous flowers of an inflorescence opens, usually at about four o'clock of a sunny morning, remains open for an hour or two, and closes again. One of the stamens borne on its pendulous stalk may be left protruding after the flower has closed, and swinging in the air scatter pollen which chance and the breeze may carry to the tassel-like stigma of another open wheat flower. Deposited there the pollen may fertilize the flower. If not, the pollen of stamens shut in by the closing of the flower serves to pollinate the stigma of its own flower. Thus self-fertilization is effected and seed is presently set.

The young grains, one of which is to be found in each of the many fertile flowers of the flowering shoot, swell, and later, as ripening progresses, become less and less watery, until, when the corn is yellow ripe and ready for harvesting, the grains are found to have the same constituents in very much the same proportions as those which were sown; a little more water, which may be lost in the final stage of ripening, a little variation, perhaps, in the amount of protein and other constituents, but on the whole the same. The wheat is cut and harvested and the plant dies. Grown in this manner it behaves as an annual. Yet wheat and many other so-called annuals may be caused to live for more than one year, either by preventing the production of flowers or suppressing them

as soon as they are formed. Mignonette, for example, generally flowers and dies within a few months from the sowing of the seed; but it may be made to live for several years if the flower-buds are picked off as they appear. It is true that frost may cut it down, but that accident may be prevented and the plant made into a perennial.

The truth is that what is called an Annual is a plant which dies after it has set seed. If prevented from seeding it may continue to live for more than a year. In many cases the life-history of a once-seeding plant is compressed within a year and it is conveniently described as an Annual; but in other vegetative growth may continue for many years, and it may be, as with certain palms and agaves, nearly a century before a once-flowering plant is ripe to flower. When that hour arrives the bloom opens, seed is set, and the plant dies. All once-flowering plants, whether ephemeral, annual, or long-lived, may be described as monocarpic, to distinguish them from polycarpic plants which do not die after flowering, but continue year after year to bear flower and fruit perennially. Monocarpic plants include biennials, e.g. those of the cabbage tribe. Their span of life is confined within a two-season period. In the first year the plant forms large quantities of food-material, which may be stored in special organs such as the onion bulb or the tuberous root (part root, part stem) of turnip and mangold-wurzel. In the second year the stores of reserve food-material are used up in the formation of flowers, seed, and fruit, and the plant dies, though no one knows why, leaves wither, stems become brittle and break, roots rot, and only the seed—the guarantor of the future of the race—remains alive.

To complete the history of the wheat plant, account must be taken of the harvest which it yields. The world's wheat-crop is grown in wellnigh every country from within the Arctic circle to the highlands under the Equator. Every month of the year sees fields yellow with ripening corn. The wheat-fields cover some 400,000 square miles—about three

times the area of the British Isles. The yield varies within wide limits, for not all soils are equally fertile nor all climates equally propitious, neither are all kinds of wheat equally prolific, nor is there always enough labour or skill bestowed on cultivation. All manner of pests take toll of the crop—from parasitic fungi such as the rusts, which check the production of grain, to flocks of sparrows, which harvest it on their own account. In favourable years small areas of highly cultivated and very fertile land have been known to yield forty-fold. From three bushels (of 63 lb.) of grain sown to the acre, 117 bushels have been harvested. In the British Isles, where the standard of cultivation is so high that it is rivalled only by Germany and excelled by none save Belgium and Holland—where, however, but small acreages are sown—the average yield over a period of recent years is 32 bushels per acre. The average for the world is 13 or 14. On the basis of 13 bushels to the acre the wheat harvest amounts to some 3,500 million tons. To estimate the total feeding value of the wheat crop it would be necessary to take into account the yield of straw, the weight of which amounts to rather more than that of the grain: for straw has no small food value, and when properly used it is returned to the land as manure, which adds greatly to soil fertility. But since the present object is to obtain no more than a rough indication of the magnitude of the wheat plant's contribution to food-supply the straw may be left out of account, as may also the seed-corn from which the harvest is raised. Calculation based on the composition of the wheat grain (Table I) and on the total yield shows that the world's crop contains nearly 70 million tons of carbohydrates, 12 million tons of proteins, of fats rather less than $1\frac{3}{4}$ million tons, and of mineral substances (ash) rather more.

It remains to form a rough estimate of the food value of the crop. Food values are measured in terms of units known as calories. A large calorie connotes the amount of heat required to raise the temperature of 1,000 grams (= 1 kilo-

gram = 2·2 lb.) of water from 0° C. to 1° C. As stated in Table I, the calories potential in one pound of wheat grain are 1,625. A man doing a moderate amount of physical work requires, if he is to maintain health and weight, enough food to supply him with 3,000 calories a day. Needless to say the diet must contain all the different kinds of food-material—carbohydrates, proteins, &c.—in suitable proportions. There must be vitamines also. But if man could and did live by bread alone, the 98½ million tons which constitute the wheat crop of the world would provide a year's sustenance for wellnigh 300 million men. This is the contribution of the wheat plant to the feeding of mankind.

III

The manufacture of food-materials by the green plant. The raw materials: mineral salts, water, and carbon dioxide. Absorption of water and mineral salts by the root. Water- and sand-cultures. The source of nitrogen to the ordinary green plant and to leguminous plants. Root-nodules and nitrogen fixation. Absorption of carbon dioxide by the green leaf. The root, stem, and leaf in relation to the work of assembling raw materials.

THE manufacture of food-materials by the green plant comprises three stages which, though they go on simultaneously, may be considered separately. As in a factory for industrial manufacture, so in the cosmic factory of the green plant, the phases of manufacture are: the assembling of raw materials, the working up by chemical or other means of the finished products, and distribution to the consumer or to middlemen. The assembling of the raw materials forms the subject of the present chapter; the working up, distribution, and also the use of the finished products that of later chapters.

The raw materials utilized by the green plant can only be obtained from the outer world. The seed from which the plant arises—the alternative source of supply—contains but little of them, and is in any case too small to hold enough to meet the requirements of the adult plant.

A step towards discovering the nature and origin of the raw materials used by the plant may be made by ascertaining the ultimate composition of plant tissues; that is, the amount of each of the chemical elements of which the tissues are composed. Analyses of different parts of plants, seeds, stems, tubers, and leaves (Table II) show that these diverse tissues contain the same chemical elements. They are: carbon, oxygen, hydrogen, nitrogen, and certain mineral elements, of which the chief are sulphur, potassium, magnesium, calcium,

phosphorus, and iron. These elements, together with nitrogen, represent the ultimate components of plant tissue, though of course they exist in the plant not in a free but in a combined form. Of them carbon occurs in the largest quantity. Nearly one-half (46·1 per cent.) of the residue left after drying wheat grain at 100° C. until no more water is lost consists of carbon.

TABLE II

	Carbon.	*Hydrogen.*	*Oxygen.*	*Nitrogen.*	*Ash (mineral substance).*
Wheat Grain	46·1	5·8	43·4	2·3	2·4
Rye Straw .	49·9	5·6	40·6	0·3	3·6
Potatoes .	44	5·8	44·7	1·5	4
Leaves of Red Beet	38·1	5·1	30·8	4·5	21·5

The remainder is made up of a relatively large quantity (43·4 per cent.) of oxygen and relatively small quantities of hydrogen, nitrogen, and mineral elements. Most other plant tissues contain the same elements in much the same proportion; leaves, however, significantly enough, contain a far higher proportion of mineral elements.

On the basis of these facts any one might make a shrewd guess as to the source whence the plant derives its supplies of raw material. The mineral salts can only be derived from the soil. Water, of which roots absorb so much, might account for a large part of the oxygen and hydrogen. Nitrogen and carbon might be obtained either from the soil or the air or from both.

Guesses of this kind, dubious though they must be, are much nearer the truth than were the conclusions based on carefully conducted experiments made before the days of modern chemistry. For example, early in the seventeenth century an enterprising and inquisitive pioneer of plant physiology, Van Helmont (1577–1644), set out to ascertain the nature of the material from which all the different constituents of plants are compounded. To do this he planted a stout willow branch weighing five pounds in an earthen vessel containing 200 pounds of closely packed soil which

had been dried in an oven. On the top of the vessel was a perforated cover to exclude dust and to permit of watering. The experiment lasted five years, and during that time nothing but pure distilled water or rain-water was given to the plant. Yet it flourished, and was found ultimately to weigh 169 pounds, *164 pounds* more than at the beginning of the experiment. The soil, on the other hand, when dried, weighed *two ounces* less than 200 pounds—its weight when the experiment was started. Ignoring the small decrease of the dry matter of the soil, Van Helmont concluded that water is the nutritive principle or mother substance which gives birth to all the components—wood, bark, and root—of which the plant is composed. Nor is the conclusion surprising when it is remembered that Van Helmont lived and experimented more than a hundred years before the birth of modern chemistry. In his day the composition of the air was unknown, and hence it could hardly occur to him to take account of supplies which might have come to the plant from the atmosphere. The nature of oxidation was undreamed of. The chemical elements had not been discovered, nor had it been established that when chemical change takes place the elements themselves remain unchanged, merely entering into new combinations. Men of science of Van Helmont's time were prepared to believe that one substance—water—could give birth to all the varied materials which the plant contains.

The discovery that mineral substances are essential to the life of plants only came after Lavoisier, in the latter part of the eighteenth century, had laid the foundations of modern chemistry, and when on those foundations methods of chemical analysis had been elaborated and applied to the study of plants. Then it was discovered that there is a large significance in the small loss of two ounces undergone by the soil used by Van Helmont in his famous experiment. It was shown, for example, that if seedling plants are grown with their roots in pure water there is no increase in the mineral constituents

of the seedlings, and the plants soon cease to grow and presently die. This discovery, which, like many another, had been anticipated by earlier workers, was made in the opening years of the nineteenth century ; and, also like many another discovery, took half a lifetime before it gained general acceptance.

When in the thirties of the nineteenth century the fact that mineral substances are essential to the life of plants became part of the common stock of knowledge, attention was directed to finding out which of the many mineral elements contained in the soil are essential to plant life and which are not. Plants themselves, even when subjected to analysis, give no certain answer. Upon occasion they may contain an extraordinary variety of mineral substances. Traces of so many as thirty-one mineral elements have at one time or another been found in the ash of plants, and among them such comparatively rare elements as tin, lead, copper, silver, mercury, and iodine. The fact that it may contain so many elements suggests that the green plant has no unerring power of absorbing only those mineral compounds which are useful to it, but that like Autolycus the green plant is ' a picker-up of unconsidered trifles '.

Comparison of the results of analysis of many different plants carries the inquiry a step farther. Of the thirty-one mineral elements which have been found in plant-ash, nine only are invariably present. They are sulphur, potassium, calcium, magnesium, phosphorus, iron, sodium, silicon, and chlorine. There are, however, two other elements which, although they do not occur in plant-ash, must not be lost sight of in the inquiry. Ash is produced by burning the dried plant, and in this process both carbon and nitrogen are driven off in combined form. They, no less than the nine elements always present in plant-ash, must be taken into account ; for both are essential, and either or both might conceivably be obtained from the soil. There is no need to be so careful with respect to the other two elements, oxygen and hydrogen ;

for since plants cannot be grown without water, and since water is composed of oxygen and hydrogen, the fact that they are essential may be at once conceded.

The investigation which has now to be made may be stated thus: Which of the elements—carbon, nitrogen, and the nine constantly occurring mineral elements—are essential to plant life, and of them which are supplied by the soil? All occur in greater or smaller quantity in soils in the form of mineral salts or other compounds, but two of them—carbon and nitrogen—also occur in the atmosphere, the one as carbon dioxide and the other as gaseous nitrogen.

The method by which this problem is solved consists in using as the medium for the growth of green seedlings some material which yields none of these elements—in fact nothing but water—and adding to this medium compounds of nitrogen and of the nine universally present mineral elements. Some preliminary trouble must be taken to make sure that the compounds selected are acceptable to the plant, for plants absorb a given element from one compound more readily than from another. Each substance added to the indifferent medium must be both soluble and suitable. The medium in which the roots are grown may be water or pure quartz sand. To it are added suitable salts of all the nine mineral elements together with compounds of nitrogen. In these conditions the plants thrive as well as in soil. Another culture is set going from which compounds of one of the elements are omitted and so on for each of the elements. In this way it is discovered that a green plant thrives perfectly and sets seed copiously (cf. Fig. 12, 'Normal') when it is grown in a water- or sand-culture to which are added the elements contained in a solution made up of:—

SOLUTION FOR WATER- OR SAND-CULTURES.

Water	1,000 c.c.
Calcium nitrate	1 grm.
Magnesium sulphate	0·25 grm.
Acid potassium phosphate	0·25 grm.
Potassium nitrate	0·25 grm.
Ferric chloride	a trace

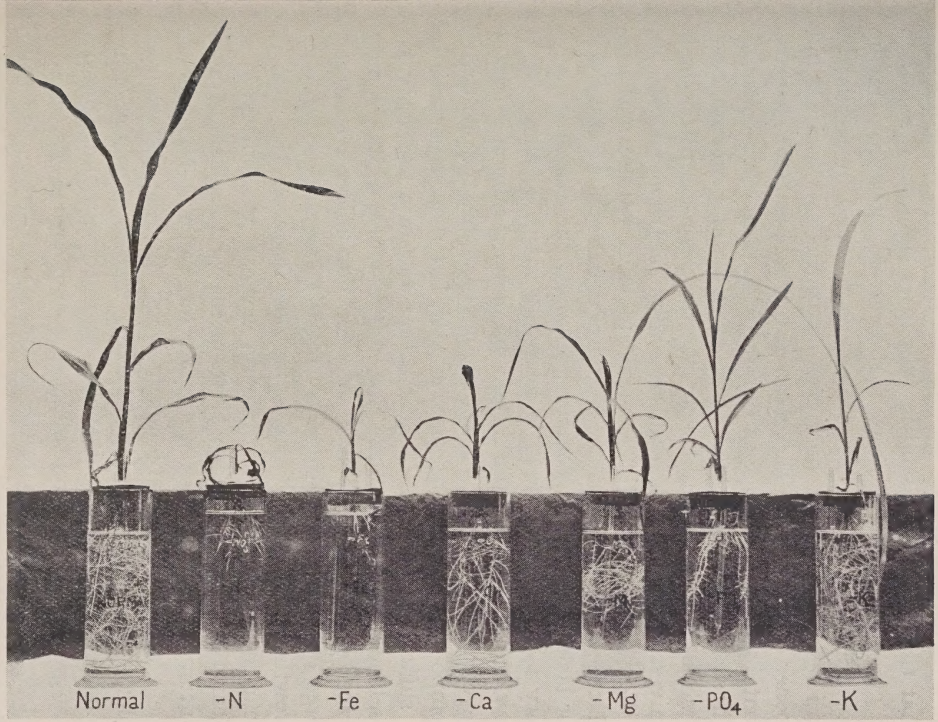


FIG. 12. Water-cultures of maize (*Zea Mais*), showing effect of withholding one or other of the essential mineral substances; Normal = complete culture solution; –N solution lacking nitrogen, and so on.

It will thrive no less if iron is supplied in some form other than ferric chloride, e.g. iron phosphate, but experiment shows that the chloride is useful in helping to suppress the growth of green algae and bacteria in the culture medium. On the other hand, if any other element enumerated in the list be omitted the plant not only does not thrive (see Fig. 12) but sooner or later dies. Therefore, of the nine mineral elements contained in plant-ash six are essential and three non-essential. The six essential elements are sulphur, potassium, calcium, magnesium, phosphorus, and iron ; the three non-essential, albeit universally present, elements are sodium, chlorine, and silicon.

Each of the essential elements plays a definite and irreplaceable role in the plant. Excess of one does not compensate for lack of another. Moreover, although the quantity necessary for vigorous growth is relatively small, a falling off of any one of them below a certain minimum results in defective development, so that it is not enough to supply the plant with compounds of each essential element, but there must also be a sufficiency of supply. The actual amounts necessary for healthy growth differ in the case of different elements. A mere trace of an iron compound suffices ; but unless a relatively large quantity of a suitable nitrogen compound be supplied growth is checked. The symptoms induced by lack or deficiency of an essential mineral element are sometimes so clear that the knowledge of them may be applied to agricultural practice. Lack of nitrogen (cf. Fig. 12, –N) results in the puniest of growth ; insufficiency, in pale yellow-green foliage and poorly developed leaves. Excess of soluble nitrogen compounds in the soil evokes, on the other hand, excessive leaf-growth. Lack or insufficiency of potash leads often to a brown spotting or a brittle rustiness of leaves : a plentiful supply of potash causes plants to go on growing and to remain green longer than usual, and enables them to withstand periods of drought. Insufficiency of phosphorus is indicated by poor root-development and light yield of flowers, fruit, and seed. Lack of iron—which, however, occurs but rarely in Nature—

is exhibited in a remarkable manner. In water-cultures supplied with all the other ingredients of the culture solution save the trace of iron salt, the leaves become chlorotic, that is, of a sickly white or yellow colour. They develop no chlorophyll, and the plants fail to grow. So small is the amount of iron necessary to encourage the development of chlorophyll that it rarely happens that the first leaves produced by a plant growing in an iron-free culture solution fail to become green. They derive enough iron from the traces present in the seed to complete the development of chlorophyll in these leaves; but that being exhausted, the later-formed leaves are devoid of green pigment. If, however, the white or yellow leaves are painted with a weak solution of an iron salt they turn green and the plant lives. The white patches of variegated leaves (pelargonium, maize, &c.) so common in cultivated plants cannot, however, be caused to turn green by this means. Variegation, unlike chlorosis, is not due to lack of iron in the soil but to some internal defect in consequence of which the chloroplasts—the bearers of chlorophyll—fail to develop properly, and this defect may be handed on from generation to generation.

When the chemistry of the living plant is considered the indispensability of the six mineral elements is by no means surprising. Potassium, sulphur, and phosphorus, as well as nitrogen, all enter into the composition of proteins or their derivatives, which constitute a chief part of the living fabric—the protoplasm. Magnesium is a constituent of the green pigment (chlorophyll), iron has been shown to be indispensable for the formation of chlorophyll, and calcium enters into the composition of young cell-walls.

Of the essential mineral elements there are but four which are apt to be deficient in cultivated soil. They are nitrogen, phosphorus, potassium, and lime. It is a common practice to remedy deficiency of one or more of these elements by adding to the soil artificial manures or fertilizers, composed of salts or other compounds of them—sulphate of ammonia,

or nitrate of soda, to supply nitrogen; basic slag, superphosphate, or bone meal, &c., to supply phosphorus (and incidentally lime); and kainit to supply potash. Lime also is frequently added, but generally in order to ameliorate the physical condition of the soil rather than to make good deficiency, albeit that sandy and peaty soils are apt to be deficient in lime. Gardeners, however, need to use lime with discretion, for certain plants—rhododendrons, azaleas, foxgloves, most heaths and other peat-loving plants—are intolerant of more than a very small quantity of lime in the soil, and show their intolerance first by a yellowing of the leaves and later by dying.

The results of water- and sand-cultures demonstrate that the green plant obtains nitrogen and other essential mineral elements from compounds supplied in solution to its roots. They show no less clearly that the plant has some other source of supply of carbon, for it thrives perfectly in water from which all compounds of carbon—except the mere traces of carbon dioxide dissolved in the water—are excluded. The problem of supply of carbon compounds to the green plant will be considered immediately, but before that is done a striking peculiarity exhibited by certain green plants deserves notice.

If the subject chosen for water-culture experiments happens to be a bean, pea, or other leguminous plant, the result of withholding nitrogen from the culture solution will be as disastrous as is the case of any other kind of green plant. But if the experiment is carried out in pure sand, and the plant supplied with a solution containing all the essential mineral substances with the exception of nitrogen, the result may be surprising. For some time the plant, deprived of nitrogen compounds, languishes and makes scarcely any growth; but after a while it may begin to improve, recover completely, grow away vigorously, and become healthy and prolific. Under conditions of sand-culture this may or may not happen, but it certainly will occur if

a little garden soil—a gram or two—is shaken up with pure water and poured on the sand.

Simultaneously with the recovery of the languishing plant it may be observed, on pulling it up, that numerous swellings (nodules) are being formed on the root (Fig. 13). The swellings are similar to those which may be seen on the root of any bean, pea, gorse, or laburnum, &c., grown in the open. No such swellings occur on the roots of leguminous plants grown in water-cultures, nor are they present in sand-cultures of leguminous plants which, as often happens, fail to grow vigorously. The vigorous growth of the bean or other allied plant in water-cultures containing the essential mineral elements, and also suitable compounds of nitrogen, shows that, like any others, leguminous plants may obtain supplies of nitrogen from the compounds contained in the rooting medium. In these circumstances the roots produce no

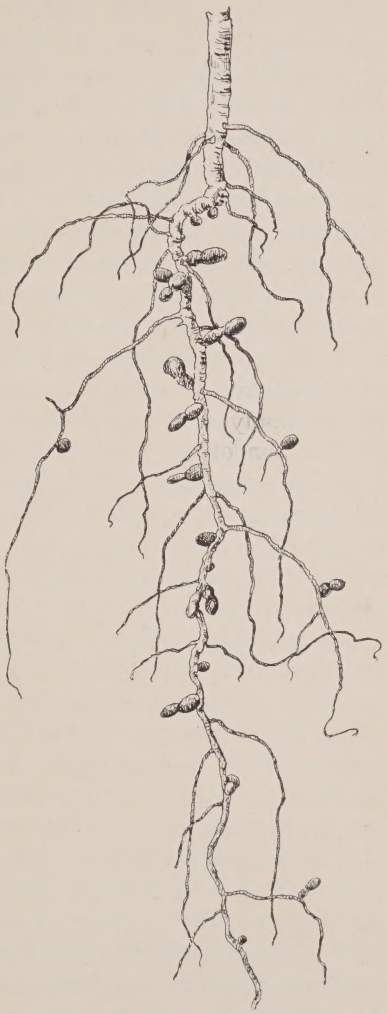


FIG. 13. Root nodules of the pea (*Pisum sativum*).

nodules. The no less vigorous growth in sand-cultures containing no nitrogenous compounds but 'infected' with a little soil demonstrates that the members of this family (Leguminoseae) stand in peculiar and wellnigh unique relation to nitrogen. If they develop root nodules they thrive even though the soil lack nitrogen. Yet, as analysis shows, the tissues of plants grown in 'infected' sand-cultures containing the merest traces of nitrogen compounds are rich in nitrogen. It follows therefore that members of this family possess means, not vouchsafed to the generality of green plants, of obtaining nitrogen from the only other available source—the atmosphere—and that they can avail themselves of this supply only if their roots bear nodules. Microscopic investigation of the root shows that the nodules consist of root-tissues the cells of which contain large numbers of a living organism—a species of bacterium (*Bacterium radicicola*). This organism exists in the soil, and is so widely distributed in cultivated ground that a little soil suffices as a source of infection of the roots of a leguminous seedling. The infecting organism enters a root-hair (see p. 57), grows through it into contiguous cells, inducing in them an excess of growth which expresses itself as the nodule. Ensconced in cells of the root the nodule organism derives supplies of carbohydrates from them, but nitrogen it obtains from the air circulating around the root. The free nitrogen it brings by ways unknown into combination, and the nitrogen compounds which it produces the nitrogen-fixing bacterium shares with and bequeaths to the leguminous plant in which it has found harbourage.

With such an unlimited source of supply the members of this happy family are insured against risk of nitrogen insufficiency, which risk hangs like a sword of Damocles over most other families of plants. The rest ever abide the question of shortage of nitrogen; the legumes are free. Partnership (symbiosis) with the nodule organism absolves them from want.

Although the discovery of the nodule organism—its symbiotic relation with the roots of leguminous and certain

other plants and its power of fixing atmospheric nitrogen—was made not more than fifty years ago, the beneficent effects of vetches and other leguminous crops on the ground in which they are cultivated had been known for centuries. The Romans were alive to the fact that cereal crops grow better on ground which has been under vetches the year before, and they used the knowledge in their system of rotation. The discovery of the part played by the nodule organism provides the explanation : for, when the land previously under vetches or other leguminous crops is ploughed, the stores of nitrogen compounds contained in the roots are distributed throughout the soil and become available for the next crop.

The fixation of nitrogen by leguminous plants is made use of in the reclamation of light sandy land, which in its natural state is too poor to be used for agriculture. After it has been dressed with artificial fertilizers and cropped with lupins the land becomes capable of supporting other crops, and so it may be brought gradually into a fairly fertile state.

It has now been shown that the essential mineral substances required by plants are derived from the soil ; but it remains to consider the way in which the root absorbs them. It is not difficult to understand how a submerged water-plant—a seaweed, for example—obtains supplies of these substances. The whole surface of the plant is bathed with water containing salts in solution, and any of these salts—or rather, any of their component ions—to which the living wall opposes no barrier may enter the plant. But the land plant has a less simple problem to solve. The mineral substances which it must obtain are contained in the soil solution; that is, in the microscopic films of water which surround the innumerable, minute particles of which soil is composed. If a root were to stay always in one place it would soon exhaust the supplies of water and mineral salts in its immediate neighbourhood. It is true that capillarity and diffusion would gradually bring about a redistribution of water and mineral salts from regions out of reach to those within range of the root. But diffusion

is a slow process, and the plant might die of drought and starvation before fresh supplies reached it.

The root, moreover, has other work to do beside absorbing water and salts. It needs must fix the plant firmly in the soil. The way in which it combines these two functions illustrates the elegance of Nature's handiwork. The older parts of the root having become wedged by growth fast in the soil and having ceased to grow are as immobile as anchors, and like anchors hold the plant. The young tips of roots, on the other hand, although their rate of movement is slow, possess an eel-like mobility. When they find themselves in soil of fine texture they grow on in a straight line. But any obstacle, a stone for example, may cause the root-tip to be deflected from its course. Soon however, when the obstacle has been circumvented by the growth of the part of the root just behind the tip, the latter is brought once again into and maintained on its original straight course.

What is called the root is, moreover, a complex system. In many plants it consists of a tap-root which grows vertically downward, a series of lateral or secondary roots which grow not vertically but obliquely downward, and sublaterals or tertiary roots borne on the laterals each of which grows out in any direction horizontally, downward, or even obliquely upward. By this disposition every inch of soil within range of the roots is explored, and every day by the continued growth of the zone behind the root-tip new areas of soil are reached by the roots.

Only a small part of the work of absorption of water and mineral salts is done by the general surface of the root system : indeed, the surface layer of the older parts of roots is corky and impervious to water. The main part of the work is performed by special organs of simple construction, but none the less of great efficiency. They are the root-hairs. Just behind the growing region of a root, an inch or so from the tip, is a zone—the root-hair region—extending backward over the root for one or two inches and covered with whitish, hair-like out-

growths. Although each single root-hair is too delicate to be seen by the unaided eye their number makes them visible. Each (Fig. 14) consists of a fine tubular outgrowth of a cell of the surface layer of the root. Through the thin, delicate cell-wall of the root-hair, the surface of which makes contact with the soil particles, water and mineral salts enter the plant. The root-hairs are often but by no means always ephemeral structures; but even though one crop of them may live no

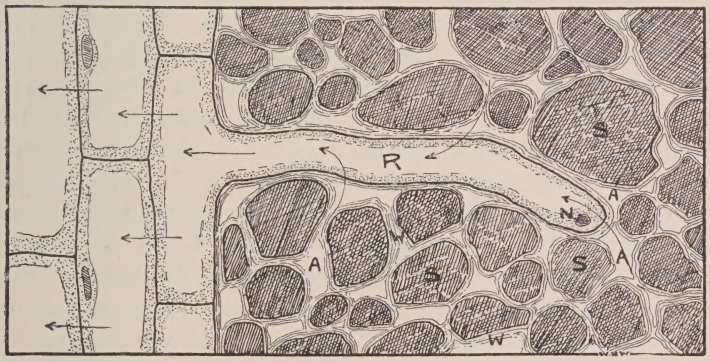


Fig. 14. Root-hair (enlarged and diagrammatic). S, soil particles; W, water films; A, air spaces; R, root-hair, showing cytoplasmic layer and nucleus N. The arrows indicate the passage of water from water films into the root-hair cell and thence through cortical cells towards the wood-vessels.

more than a day or two it is succeeded by another borne always in the same relative position, namely, a little way behind the region of elongation. That they are the absorbent organs may be proved in many ways, and may be inferred from the fact that the more difficulty a plant has in obtaining supplies of water and mineral salts the more root-hairs are apt to be developed. Thus some aquatic flowering plants possess none. The roots of tulips grown in soil or moist air develop normal root-hairs, but when grown in water they produce, not elongated hairs but slight cellular bulges, not visible except when sections of the root are examined micro-

scopically. The fatal effects of exposing roots of young plants to dry air are in part due to the withering of the delicate root-hairs. Deprived of their activity the plant, when set in the soil and exposed to air and sun, is unable to absorb enough water to replace that which is lost by the leaves; it dies before new roots with fresh outcrops of root-hairs have had time to develop.

The fact that leaves (see Table II, p. 45) are so rich in mineral salts indicates that these materials which are absorbed by the root pass to the leaves. The course followed from root to leaf may be demonstrated accurately in various ways, and may be inferred from the result of a very simple experiment. If, preferably on a sunny day, an herbaceous plant with a fairly transparent stem—e.g. balsam (*Impatiens noli-me-tangere*)—be cut off at ground level, and the cut end of its stem immersed in a watery solution of eosin or other soluble dye, it will not be long before the woody bundles of the stem and their fine endings, the veins of the leaves, become deeply stained. As with the dye, so is it with the mineral salts absorbed by the root. They pass in solution through the tissues of the root, arrive at and enter the young vessels, rise with the water current in the cavities of the vessels up the root to stem, and from stem to leaf, until having entered the vessels of the leaf-stalk, they pass ultimately into the fine veins which run through all parts of the leaf. The cells surrounding the finest veins absorb the water and salts and distribute them throughout the tissues of the leaf. But inasmuch as the cellular tissues of a plant form a continuous system, all cells of all parts of the plant receive in time some of the mineral salts absorbed by the roots, and thus have at their disposal supplies of these essential food-materials.

It remains to consider how supplies of carbon are obtained. The green plant, although nearly one-half of its dry weight consists of carbon, flourishes and sets abundant seed when grown in a culture solution (see p. 48) which contains no

carbon compounds. The conclusion is therefore inevitable that supplies of carbon compounds are obtained not from the soil but from the atmosphere, the only other source open to it. This conclusion, when first announced in the early part of the nineteenth century, was received with scepticism. It seemed to put too great a strain on credulity; for the atmospheric source of carbon can only be carbon dioxide, and the proportions in which this gas occurs are no more than three or four parts in 10,000. Those who raised this objection forgot, however, the vastness of the atmosphere, nor was it comprehended in their day how remarkably efficient are the leaves of green plants in absorbing gases from the atmosphere. Estimates of the extent of the atmosphere show that the store of atmospheric carbon dioxide is amply sufficient to supply the daily needs of vegetation. Every fire that burns augments it, every breath that is breathed by an animal adds to the store. Carbon dioxide is, moreover, one of the end-products of decay, and even plants—both green plants and non-green fungi and bacteria—contribute throughout their lives and in their death to the stock of atmospheric carbon dioxide. Furthermore, experiment shows conclusively that the carbon contained in green vegetation is derived from the carbon dioxide of the atmosphere, and so the bold and widely discredited conjecture made in the eighteenth century by the first and greatest of British plant physiologists, Stephen Hales (1677–1761), that 'somehow air is wrought into the composition of plants', has become an accepted fact.

It may be shown, for example, that a healthy plant rooted in good soil ceases its manufacturing operations and stops putting on weight (dry weight) immediately it is cut off from supplies of carbon dioxide. It may also be demonstrated experimentally that leaves absorb atmospheric carbon dioxide. For this purpose advantage is taken of the fact that fresh baryta water absorbs carbon dioxide and unites with it to form an insoluble, white compound (barium carbonate); so that the presence of carbon dioxide in air

bubbled through it is betrayed by the milky appearance taken on by the baryta water. A wide glass tube (Fig. 15) is connected at one end with 'potash bulbs' containing fresh baryta water, and the farther end of the potash bulbs is connected with an aspirator—an apparatus which serves to draw a current of air through vessels in air-tight connexion with it. The apparatus is placed in a sunny room, and when all is ready the glass tube is packed loosely with fresh green leaves, baryta water is added to the potash bulbs, and a slow current of air is drawn through the apparatus. The air which

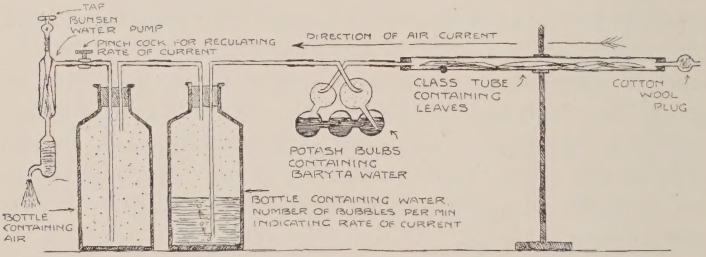

TAP
BUNSEN WATER PUMP
PINCH COCK FOR REGULATING RATE OF CURRENT
DIRECTION OF AIR CURRENT
GLASS TUBE CONTAINING LEAVES
COTTON WOOL PLUG
POTASH BULBS CONTAINING BARYTA WATER
BOTTLE CONTAINING WATER. NUMBER OF BUBBLES PER MIN INDICATING RATE OF CURRENT
BOTTLE CONTAINING AIR

FIG. 15. Apparatus for demonstrating the continuous absorption of carbon dioxide by illuminated green leaves (see text).

has passed over the sunlit green leaves causes no milkiness in the baryta water. The carbon dioxide which it originally contained has been removed by the leaves.

That living leaves only possess the power of continuing to withdraw carbon dioxide from the air may be shown by replacing them by leaves which have been killed by hot water. The gradual clouding of the baryta water indicates that leaves when killed do not continue to extract carbon dioxide from the air-current passed over them. Nor are the white parts of variegated leaves more efficient than dead leaves. If variegated leaves be cut up and the white separated from the green parts it may be shown that whereas the latter extract carbon dioxide from the air-current, the former do not. The experiment with the living green leaves may be

continued throughout the hours of daylight without sign of milkiness appearing in the baryta water. During this time large quantities of carbon dioxide have been absorbed, yet there is no proportionate accumulation of carbon dioxide in the leaves. Some indeed of that absorbed by the chlorophyll is held by it, but the bulk of the carbon dioxide taken in from the air has disappeared from the leaf. It has undergone chemical change.

Herein lies the explanation of the fact that absorption of carbon dioxide by the living green leaf exposed to light goes on continuously. Carbon dioxide may pass into the dead leaf as readily as into the living green leaf; but the former lacks the power to decompose it. Hence equilibrium in carbon dioxide content is soon reached and no more of the gas is absorbed. But with the living leaf exposed to sunlight, equilibrium of carbon dioxide content between it and the atmosphere is never reached so long as the carbon dioxide absorbed is changed chemically by the green tissues, and hence the process of absorption may go on continuously throughout many hours of the day. If, however, the green leaf be prevented from using carbon dioxide, absorption soon ceases. For example, if a black cloth be thrown over the glass tube containing the green leaves, the rapid and dense clouding of the baryta water indicates that carbon dioxide has not only ceased to be absorbed but is actually being liberated by the leaves (see p. 140). Remove the cloth so that the leaves are exposed again to sunlight, and a fresh solution of baryta water put in the place of that which has become milky remains clear.

The experiments carry us—as all experiments should—farther than we had thought to go. They show that not only is atmospheric carbon dioxide the source whence the plant derives carbon, and that the green leaves are the agents which effect absorption of carbon dioxide, but also that they transform it, if light be present to assist the transformation.

The nature of the change brought about by the green leaf and sunlight will be considered presently; but immediate

attention must be given to the question, How is it that a green leaf is so efficient an absorber of carbon dioxide? It is true that leaves present a large surface to the air, and that their delicate poise on an elastic stalk serves like a fan to keep up a constant movement of the air about them, so that fresh supplies are continuously brought within their neighbourhood. It is true also that the air itself is never still—winds and the heat of the sun disturb it. Yet, on the other hand, the surface of the green leaf appears to be continuous. The cells which constitute the surface layer (epidermis), though delicate, are generally in continuous touch with one another; and curiously enough the outer walls of the epidermal cells often consist not only of cellulose but also of varnish-like substances (cutin), which help to make them impermeable to air as well as water. The under surface of a green leaf is indeed more delicate than the upper; the external walls of its epidermal cells are less cuticularized, so that it offers less opposition to the passage of carbon dioxide than does the upper. It would seem, however, a strange contradiction that a leaf, an essential function of which is to absorb large quantities of carbon dioxide, should—especially if it be leathery, as are so many leaves—put half its surface (namely, the upper surface) more or less out of action by waterproofing it over with a cuticular layer which checks the diffusion of gases into the leaf. But all life is a compromise, and the explanation of the apparent contradiction is, first, that even when heavy cuticularization prevents the upper surface from playing its part in absorbing carbon dioxide the work is still discharged effectively by the under surface; and, second, that leaves have more than one kind of work to do. Besides absorbing carbon dioxide and radiant energy they have also to provide that the sun's rays do not damage the delicate tissues of the leaf or cause them to lose water faster than they are able to obtain it from the roots.

This aspect of the problem of leaf-structure and leaf-adaptation is, however, so important that it must be left for

further consideration (see Chap. VII). For the present, attention may be confined to discovering how it is that the apparently continuous surface of the leaf admits carbon dioxide readily and in large quantities. The truth is that the leaf-surface is *not* continuous. That this is so may be shown both by microscopic examination and by direct experiment. If a rubber tube be attached to the stalk of a delicate leaf, the blade of which is submerged in water, a mere blowing at the open end of the tube may suffice to drive fine bubbles of air out of the leaf. Or if the rubber tube, fixed securely to the leaf-stalk, be attached to an aspirator, water may be sucked into the leaf, and, replacing the air contained in the spaces in the green tissues, cause the submerged blade to assume a darker and more translucent colour. Since air or water in mass may be made to pass across the uninjured surface of a leaf, it follows that that surface contains holes, and that the holes provide free communication between the outer atmosphere and the inner atmosphere—that is, the gases contained in the spaces between the cells of the leaf.

Microscopic examination of strips torn from the surface of a green leaf shows that cleft-like openings (stomatal openings, Fig. 16) occur in it. In some plants they are confined to the under surface ; in others they occur on both surfaces. The stomata are numerous. A single oak leaf contains several million. They are so minute that they may be measured conveniently only in terms of some special unit of length. The unit employed for measuring cells and such things as stomata is μ. It is equal to 1/1,000 mm., i.e. 1/25,000 inch. The pore or aperture of a fair-sized stoma may be 6μ in diameter. Seen in surface section it appears as an oval slit between two cells of the epidermal layer. The cells between which the stomatic aperture occurs are known as guard-cells. They are recognizable in surface view by their peculiar curved shape, which is markedly different from that of the ordinary epidermal cells. The latter, which are in the form of minute flat plates, larger in width and breadth than in

depth, have in some plants wavy, in others straight outlines. The guard-cells seen in surface view have each a curved outline, with the convex side of the curve away from the stomatic pore (Fig. 16). Whereas the wall of an ordinary epidermal

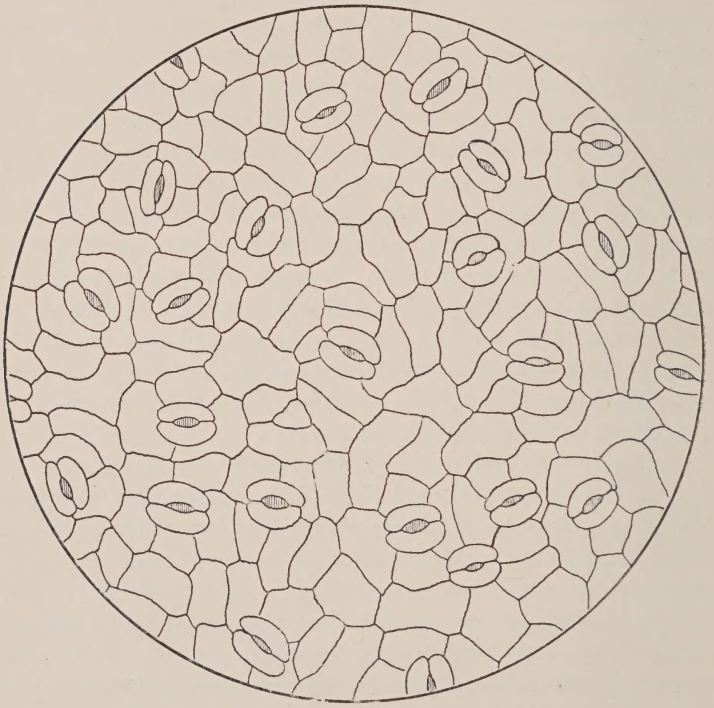


FIG. 16. Surface view of epidermis of leaf of cherry laurel (*Prunus laurocerasus*) showing stomata : stomatic pore shaded.

cell fits closely against that of its neighbour, leaving no space between, the common or party walls of a pair of guard-cells are fused with one another throughout part only of their length : the middle region of the wall of one cell is withdrawn from that of its fellow, so that a cleft-like space occurs between the cells. This space (the stomatic pore) communicates freely

with spaces within the leaf formed, as are the stomata, by the separation of the walls of contiguous and originally completely united cells. Thus, as already shown, and as indeed might be judged from their change of colour when waterlogged, the green tissues of a leaf are not compact but are honeycombed with intercellular spaces communicating freely with one another and by way of the stomata with the outer air.

With this sketch of the structure of a green leaf in mind it is not difficult to realize that diffusion of gases may take place readily between the air in the intercellular spaces and the external atmosphere. If the internal and external atmospheres are at the same temperature and pressure and contain the same concentrations of carbon dioxide and other gases, a state of equilibrium obtains and the concentration undergoes no change ; but if the concentration of one of them—e.g. that of the carbon dioxide in the internal atmosphere—falls, the rate of diffusion of that gas from the external atmosphere into the intercellular spaces will be greater than that in the opposite direction, and hence carbon dioxide accumulates in the leaf until equilibrium is re-established.

A similar equilibrium will be established between carbon dioxide pressure in the internal atmosphere and that in the green cells bordering on the intercellular spaces. It is true that these cells do not contain carbon dioxide in the form of a gas, but in solution. This, however, makes no difference, for since water has the power of dissolving carbon dioxide, if that contained in a cell loses carbon dioxide, more of the gas, diffusing in, will undergo solution. Thus the chain of events which leads to the continuous passage of carbon dioxide into an illuminated green leaf, though long, is simple. During darkness, if the stomata of a leaf were to remain open (see p. 165), equilibrium with respect to this gas would tend to be established between external and internal atmospheres. But so soon as light falls on the leaf the green cells begin to use carbon dioxide : the concentration of the carbon dioxide in solution in the cells falls : equilibrium

is disturbed, and carbon dioxide dissolved in the water in and upon the cell-wall diffuses into the cell. Then, in turn, and for a similar reason, carbon dioxide passes by diffusion from the internal atmosphere into solution in the water of the cell-wall, but inasmuch as the passage entails a disturbance of equilibrium between the internal and the external atmospheres it is followed by diffusion of carbon dioxide from the outer air into the intercellular spaces ; and manifestly, so long as the green cells continue to use carbon dioxide the diffusion gradient will be maintained, and carbon dioxide will pass continuously into the green leaf.

The stomatic pores are, however, so minute that it might be objected that the large quantities of carbon dioxide used by a green leaf in the course of a day could scarcely diffuse through such narrow channels. Experiment shows, however, that the stomata provide the channels through which the gas passes. It suffices, in order to block stomata, to smear the surface of a leaf with a thin layer of vaseline. If leaves with stomata confined to the under-side be smeared with vaseline on that side it is found that, when placed in the apparatus described previously, they fail, even though well illuminated, to extract carbon dioxide from the slow current of air drawn over them by means of the aspirator. The baryta water turns milky. But if the upper side only be smeared with vaseline the power of the leaves to extract carbon dioxide from the air is unimpaired.

It is interesting to find that the efficiency of the green leaf in absorbing carbon dioxide has led to experiments which have discovered previously unsuspected facts. Thus, if a plate of tin-foil, pierced with holes approximating in size and number to the stomatic pores of a leaf of the same area, be placed over a dish containing a solution of potash, it will be found that the rate at which the potash absorbs carbon dioxide from the air is not much less than it is when the surface of the solution is fully exposed. Thus plants, by adopting the device of extremely minute openings distant from one

another by not more than five or six times the diameter of those openings, have it both ways; they are able at once by their epidermal cells to offer protection to the delicate internal tissues, and by their stomata to get all the carbon dioxide they can use.

Thus are the raw materials which the green leaf uses assembled in it: water and mineral salts from the soil, and carbon dioxide from the air.

IV

The absorption of radiant energy by the green leaf. Chloroplasts and leucoplasts. The chlorophyll-containing tissues: palisade and spongy parenchyma. Chemical and physical properties of chlorophyll. Photosynthesis of carbohydrates: and the synthesis of organic nitrogen-compounds. Nitrifying bacteria.

THE widely branching and firmly fixed yet ever-extending root-system, with localized absorbent root-hairs, provides the green plant with water and mineral salts. The green leaves, with their broad surfaces beset with minute and numerous stomata, secure from the atmosphere ample supplies of carbon dioxide, and so in the green tissues of the leaf the raw materials are assembled. Into those tissues the rays of the sun penetrate, and by them some of the rays are absorbed. Thus the leaf is equipped with materials and energy for the work of food-production.

It might be supposed, in view of the success with which the green plant plays the part of universal food-provider, that it is a very efficient absorber of radiant energy, and that it utilizes for food-production all the energy which reaches it from the sun. Yet, truth to tell, the green leaf, like all living things, falls far short of perfection. It absorbs by no means all the radiant energy which the sun lavishes on it, and of that which it does absorb the green leaf is able to utilize but a small fraction for food-production purposes.

Of the sun's rays which fall on a leaf many are reflected from the surface, and the degree of shininess of leaves is an index of the amount reflected. The dull green surfaces of shade-tolerating plants reflect but little light; the highly cuticularized, burnished, mirror-like surfaces of leaves of the date-palm (*Phoenix dactylifera*) and other sun-enduring plants

reflect much, and in so doing mitigate the fierceness of the light to which they are exposed. Of the rays which enter the leaf some pass right through it, as witness the dappled shade cast by sunlit leafy trees. Reflected and transmitted rays alike count for nothing in the operations carried on by the plant, for only if it is absorbed may radiant energy be applied to doing work in the plant. It is the chloroplasts which are in the main responsible for the absorption of radiant energy effected by leaves; and it may be computed that a leaf of fairly delicate texture absorbs not much more than a quarter of the sun's rays which fall upon it. The energy which is gained is put to various uses. By far the larger part serves to evaporate water from the leaf: a by no means unserviceable operation so far as the plant is concerned (see p. 161). Radiant energy also plays a part, and often an essential one, in the formation of chlorophyll; it also serves to keep growth in gear.

It is probable that the different kinds of work promoted by radiant energy absorbed by the leaf are done—or are, at all events, most efficiently done—each by different rays. Chlorophyll, whilst very transparent to green light, is fairly opaque both to certain rays of blue-violet and orange-red light. When green leaves or a solution of chlorophyll are examined by means of the spectroscope the regular succession of spectral colours—violet, indigo, blue, green, yellow, orange, and red—into which the instrument resolves white light is seen to be interrupted. The blue-violet region is darker than it would be were the leaves or solution removed, and in several places both there and towards the red end of the spectrum are to be seen dark bands which indicate absorption of light. Investigation of the effects produced by the rays of different parts of the spectrum shows that, whereas either blue-violet or red-orange rays may bring about the formation of chlorophyll, the evaporation of water and the gearing of growth are effected mainly, if not entirely, by the energy of the blue-violet rays. By growing plants behind glass or other

coloured screens which cut off blue-violet light, results are produced very like those brought about by darkness. Except that they develop chlorophyll the plants suffer from similar disorders of development. Wheat and similar Monocotyledons produce long, thin, flabby leaves, and beans and Dicotyledons of like habit give rise to greatly elongated, weak stems bearing abnormally small leaves separated by extremely long internodes. On the other hand, the major part of the work of food-production is done at the expense of the energy contained in the red-orange rays, and plants grown behind screens which cut off these rays starve more or less completely.

When from the sum total of sunlight that falls upon a leaf deduction is made of reflected and transmitted rays, and of the radiant energy which is used in evaporating water and doing other kinds of work, it is found that after all the green plant only uses the energy of some one-half per cent.—say in the proportion of one out of every 200 rays which fall upon it—for establishing the food foundations of the world. Yet limited as is the efficiency of the green plant, man, so far, has not learned to do better.

The green pigments which absorb radiant energy are contained as an emulsion in the surface layer of the chloroplasts: minute living bodies which occur in vast numbers in the cytoplasm of the cells of the green parts of leaves and stems.

In the long course of evolution from algal ancestors—if, as is probable, that is their origin—seed-bearing plants have become possessed of chloroplasts very different from those of their remote forebears. Chlamydomonas (see Fig. 3) has in its single cell one large chloroplast or chromatophore; but the green plant possesses in each cell of its many-celled, green tissues large numbers of minute, more or less discoidal, chloroplasts. The cells of the leaf which contain chloroplasts form a green tissue made up of several layers. Immediately beneath the upper epidermis, and united with its cells, is the palisade tissue (Fig. 17), made up of one or two layers of cells containing numerous chloroplasts, and elongated at right angles

to the leaf-surface. Below the palisade tissue the green cells form a loose spongy tissue, which extends to and joins with the under epidermis. The cells of the spongy tissue are of an irregular, often starry shape, and each of the ray-like out-

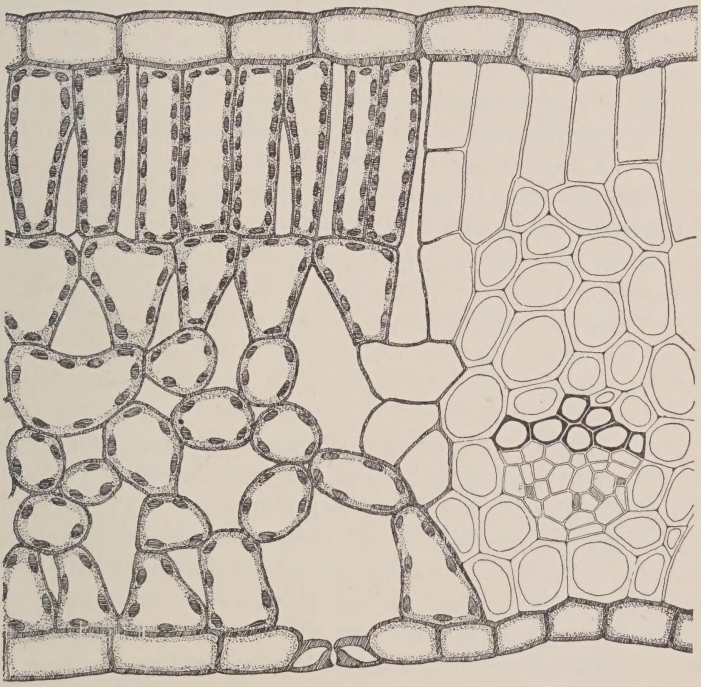


Fig. 17. Transverse section of the leaf of the beech (*Fagus sylvatica*), magnified (see text).

growths joins with a corresponding one from a contiguous cell, so that the spongy tissue is tunnelled with spaces filled with air, which is in communication through the stomata with the external atmosphere. Similar although less conspicuous intercellular spaces occur between cells of the palisade tissue.

The chloroplasts of a flowering plant may be so small as

5μ–10μ, but they make up in numbers what they lack in size. Beneath a square millimetre of the surface of a leaf, 400,000 chloroplasts may lie in the successive cells of palisade and spongy tissue. A large leaf of the castor-oil plant (*Ricinus communis*) with a surface of ten square inches contains some ten thousand million chloroplasts, all formed by the successive division and growth of one or two colourless chloroplast forerunners (leucoplasts), which were brought into the embryo by the female cell at the time when it united with the male cell to give rise to a new individual.

Inasmuch as the smaller a body the greater is its surface in proportion to its bulk, it follows that, although the amount of living material and chlorophyll contained in the chloroplasts is not large, the sum total of the surface presented by the numerous chloroplasts of a leaf is very great. At a rough estimate, based on size and number of the chloroplasts and of the leaves, the total surface of the chloroplasts contained in a well-grown castor-oil plant amounts to about an acre, and that of the chloroplasts of a single leaf to some 260 square yards—that is, five-sixths the size of a lawn-tennis court. If, therefore, as modern chemistry teaches, chemical action is apt to go on vigorously at the surfaces of things, and particularly at the relatively large surfaces of things of extremely minute size, the surface of the chloroplasts, rich in absorbed radiant energy, is likely to be the seat of intense chemical operations. It certainly provides ample room.

Like the action of a play within a play, the development of the leucoplasts keeps time with that of the embryo plant. Before the single-celled embryo divides to form a two-celled embryo the leucoplasts increase in number by division, and when cell-division occurs some pass into one and some into the other cell, and so on throughout all the divisions which lead to the formation of the recognizably plant-like embryo. So it is that every one of the multitudinous cells which compose the body of the young plant contains potential chloroplasts derived from the original two or three leucoplasts whose

descendants are as numerous as the sands of the sea. In some pines and other plants the leucoplasts contained in the rudimentary leaves and stem of the embryo turn green without waiting for light to stimulate them to chlorophyll formation; but in most plants the leucoplasts remain colourless until the seedling leaves, emerging from the seed and soil, expose themselves to light.

The change from colourless to green state is restricted to certain tracts—the leaves and young stems. In the deeper tissues of stems exposed to light, and in underground stems and roots, the leucoplasts retain their colourless state. In some instances it is easy to make them turn green by exposure to light: a potato tuber, for example, when put to sprout before planting, shows by the greenness of its underlying tissues when the brown skin is rubbed away that light has effected the change. In other cases nothing will make them green. Thus in the general epidermal cells of green leaves the leucoplasts remain unaffected by light, although in the guard-cells which lie beside them chlorophyll is formed at an early stage, and persists until the leaf grows old and past its work. Yet a plant in the course of its evolutionary changes may repudiate the ban which at an earlier stage of its career it had laid on the development of this or that of its parts: flowering plants, for example, which have reverted from the land to the water and have become submerged aquatics, likely perhaps to suffer from insufficiency of light, may bring their green tissues nearer the light by transforming the leucoplasts of epidermal cells into chloroplasts.

The influence of light on plastids is not confined to determining the formation of chlorophyll in them. Light also affects the shape of chloroplasts and the position which they take up in the leaf. In bright light the alinement of the chloroplasts in the cells of a plant is different from that which obtains in diffuse light, and different again from that assumed by them in darkness. When the sun shines brightly the chloroplasts line up in single files parallel with the direc-

tion in which light falls on them, so that they offer the least exposure to the sun's rays; but in diffuse light they change flank, and the single files lie at right angles to the light so that each chloroplast may catch every ray it can. Whether the movements are brought about by those of the cytoplasm, or whether the chloroplasts themselves move after the manner of an amoeba, is not known. In these and yet other ways does the plant make full use and take care of the swarm of chloroplasts within its green cells.

The plastids embedded in the cytoplasm of the green cell, though no doubt subject to some measure of protoplasmic control, yet enjoy powers of growth and division: a quasi-independence which leads sometimes to a strange state of affairs. A plant may be healthy and yet its plastids may suffer from debility. They do not grow and divide fast enough to keep pace with the growing and dividing cells of the plant, and in consequence some cell-tracts which should be green remain colourless, and the symptom of the debility is variegation. Variegated races occur among many kinds of plants, wild and cultivated, and their curious motley of leaf- and stem-colour—green and white or yellow in stripes or blotches—may be seen in antirrhinums, maize, pelargoniums, aubrietia, and many another plant.

The behaviour of some variegated varieties shows that chloroplasts play a fundamental part in the nutrition of plants. Now and then a variegated plant may produce a branch with uniformly green leaves, and now and then one with pure white leaves. The green branch grows so vigorously that if it be not removed there is a risk of its dominating and suppressing the variegated branches. The white branch grows weakly. If the green branch be layered, or struck as a cutting, the independent, green-leaved plant which it produces flourishes; a cutting of a white branch, however, does not grow but dwindles away; yet the pure white branch, though slow-growing, was not moribund when attached to the plant. In the latter state it may in time produce flowers and set

seed. The white branch can take food when food is to be had, but it cannot make food for itself.

The green colour of normal chloroplasts is due to a mixture of four pigments which are collectively called chlorophyll. Of these pigments two—known, the one, as chlorophyll *α* and, the other, as chlorophyll *β*—are green, the former a good green, the latter a blue green; the other two, the one yellow, the other orange in colour, are of less complex chemical constitution and are known respectively as carotin and xanthophyll. The chemistry of all four pigments is known, but the exact part they play in the manufacturing process—beyond acting as absorbers of radiant energy—is still to be discovered.

Even in the last phase, when the leaf is old and its fall near, the plastids may yet render service to the plant and mankind. The pigments of the leaf may undergo change and give rise to red and orange colours of bright hue, and so the dying year is brightened by rich autumnal tints. So also may the plastids of other parts of the plant develop similar colours. In some cases, as, for example, in the ' root ' of the carrot, the orange pigment may have no apparent significance, whereas in others, for example, in flowers and fruit, the vivid colour may serve to lure insects to pollinate the one and birds to disperse the other. Not all the bright colours of flowers and fruits, however, arise from the chloroplasts. The blues and pinky-reds and magentas, so common in them, though they serve similar ends, belong to another class of pigments—the anthocyans—and are formed by the protoplasm and not by the plastids.

To discover the part played by the chloroplast in its prime before the activities of the leaf have begun to wane has taken science several hundred years to accomplish, and even now the inquiry is not at an end. Nevertheless the fundamental role which the chloroplast plays in the manufacture of food-materials has been established, and something is known of the way in which it sets about the work.

If, just before a warm summer night is done, well-grown,

delicate, green leaves of some tree or shrub be examined after suitable treatment, there will be found remarkable differences between them and precisely similar leaves plucked from the same plant in the late hours of the morning. The leaves picked after the sun has been shining on them for some hours have more solid substance than is contained in the leaves plucked before sunrise: their dry weight is greater. It may be shown, moreover, that the increase in dry weight is due to the accumulation in the leaf of a combustible substance which, when burned, gives rise to carbon dioxide and water and liberates energy. By picking sufficient numbers of similar leaves, one lot before and others at, say, hourly intervals after sunrise, it may also be shown that as the morning wears on more combustible material is to be found in the leaves and more energy is liberated from them when they are burned. Sunlight, therefore, means to the green plant increase of substance and of potential energy. The nature of the substance to which the increase is due may be ascertained by killing a night-plucked and a similar day-plucked leaf with boiling water, placing the leaves in alcohol, and exposing them to sunlight to bleach the green pigments; then, when they have become colourless, washing the leaves with water to remove the alcohol, and placing them in a white saucer containing dilute tincture of iodine (iodine dissolved in water with a little potassium iodide). The leaf picked during the sunny morning becomes of a uniform blue-black colour—proof that it is rich in starch—that picked before sunrise remains colourless, or at most assumes a blue tinge. Microscopic examination of sections shows that the starch occurs in the chlorophyll-containing tissues and that the grains lie in close proximity with the chloroplasts.

The starch which makes its appearance in the sunlit leaves can have but one of two origins. Either it, or something which gave rise to it, comes from other parts of the plant, or it is formed in the leaf. That the latter is the case may be shown by plucking leaves before sunrise, placing their stalks in

water, and leaving them for some hours in sunlight. They are found presently to contain not less but generally more starch than is formed in leaves which remain attached to the plant.

The test with iodine may be used to ascertain the rate at which starch appears in leaves. In this way it is found that starch in recognizable quantity is produced by leaves after less than half an hour's exposure to light, and it may also be shown that during darkness its disappearance is gradual. The disappearance, however, only takes place in leaves attached to the plant. Detached leaves which have been exposed to light until they contain much starch, if kept in darkness, retain most of it for a very long time. Even though they are kept with their stalks in water the starch disappears but slowly. They have nobody to give it to, and the leaves themselves cannot use it all. It follows, therefore, that the green leaf not only makes carbohydrate for itself, but supplies the plant with the surplus of its manufacture.

The test with iodine offers a means of exploring the conditions in which starch makes its appearance. In red light, for example that transmitted by a suitable red glass screen, starch formation goes on very well, albeit less rapidly than it would if the screen were not there ; but in blue light transmitted by a screen of blue glass starch formation fails.

If in the above experiment made by applying the starch test to green leaves, variegated leaves are used, it is found that the treatment with iodine reproduces in blue and white the original, variegated, green and white pattern: where chlorophyll was, manufacture has gone on, and where it was absent there has been no formation of starch. It may also be shown experimentally that both light and carbon dioxide are essential to carbohydrate production. A plant is kept in darkness until its leaves are empty of starch. Whilst still in darkness the stomata-bearing surface of one of a pair of its leaves is smeared with vaseline along and on either side of the midrib. Both leaves are covered with tin-foil from which has been

stamped out some easily recognized pattern as, for example, the letters of a word. The plant with its stencil-covered leaves is exposed to light. In the course of an hour or two the iodine test shows that where, in the one leaf, both light and carbon dioxide reached the green tissues starch has been formed, but where, in the other, the vaseline, about the middle

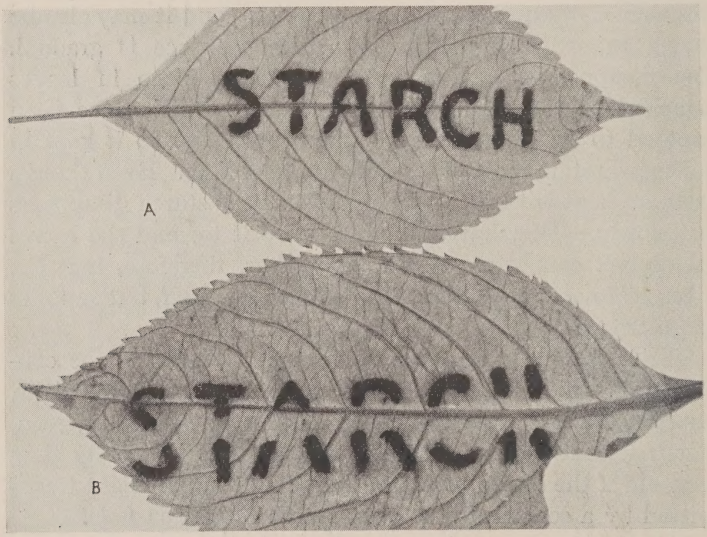


FIG. 18. The dependence of starch formation on illumination and supply of carbon dioxide—see text.

of the band of lettering, prevented the access of carbon dioxide no starch has been produced, even though that part of the leaf was illuminated (see Fig. 18 B).

The iodine test may also be used to show that, within limits, the higher the intensity of light the greater is the accumulation of starch. A leaf covered with a photographic negative which transmits more light through some of its parts than through others yields, when killed, decolorized, and treated with iodine, a print in blue and white in which the

objects photographed stand out with surprising clearness, though, needless to say, if the exposure to light be too long or too short the common faults of amateur photography also reproduce themselves.

It is less easy to demonstrate that water takes part in the manufacturing process carried on by the green leaf. It is true that starch formation is brought to a standstill when drought occurs, but in these circumstances carbon dioxide ceases to be absorbed, and the cessation of manufacture might therefore be due to a shortage of supply of carbon dioxide and not directly to insufficiency of water. Nevertheless the chemical constitution of water, carbon dioxide, and starch makes it certain that water is used, and also gives a broad hint as to the nature of the process.

Water (H_2O) and carbon dioxide (CO_2) are fully oxidized bodies: neither combines with oxygen to form a more oxidized, stable compound. On the other hand, starch if thrown into the fire burns, and as it combines with oxygen gives rise to water and carbon dioxide. The combustion may be represented by the equation:

$$C_6H_{10}O_5 + 6\,O_2 = 6\,CO_2 + 5\,H_2O$$

Inasmuch as starch when oxidized gives rise to water and carbon dioxide, it follows that for starch to be formed from them carbon dioxide and water must undergo reduction—that is, a chemical change in the course of which oxygen is lost to them.

The conclusion may be put to the test of experiment, and for the purpose it is convenient to use green, submerged water-plants. Of them none is more suitable than the American water-weed, *Elodea canadensis*. The leafy stems of several healthy green shoots are cut across to expose fresh surfaces, tied to a glass rod to keep them down, sunk upside down in a large glass vessel filled with water, and held in place by inverting a large funnel over them. The stem of the funnel being well submerged, a test-tube filled with water is placed

with its open mouth dipping under water over the open end of the funnel into which the stems project. When the apparatus is placed in bright light, bubbles of gas begin almost at once to escape from the cut ends of the stems and, rising through the water, accumulate in the test-tube. In the course of the day enough may have accumulated to permit of the gas being tested. A glowing taper plunged into it is rekindled, and this evidence of richness in oxygen may be confirmed by the application of more delicate tests for that substance. If the plant remain healthy and the water fresh, the evolution of oxygen goes on continuously for many days. It ceases at night, to begin again each morning, and is faster when the sun shines than when it is beclouded. The escape of oxygen may be checked, even though the plant be exposed to sunlight, by replacing the fresh water by water which has been boiled for a long time and cooled out of contact with air, so that it contains very little carbon dioxide: and the check is yet more complete if absorption of carbon dioxide by the water be prevented by covering the latter with a layer of light oil. In these circumstances the escape of oxygen stops entirely. On the other hand it may be caused to begin again, and to become very rapid, by placing the plants in water saturated with carbon dioxide. With a fresh and large supply of the gas the green plant almost instantly resumes manufacturing activity and oxygen is liberated once more.

By more exact methods involving gas-analysis, it may be shown that the volume of carbon dioxide used by a green plant exposed to light is equal to that of the oxygen which is evolved; from which it follows that, since all gaseous molecules occupy the same space, for each molecule of carbon dioxide decomposed a molecule of oxygen is liberated.

Consideration of the results of all these experiments with the green plant in sunlight leads to the conclusion that decomposition of carbon dioxide, evolution of oxygen, and formation of starch are all parts of the same process. The process may be

variously described. It is one of carbon assimilation ; for it results in a gain of carbon to the plant : it is an assimilation of carbohydrate, for the plant gains starch. It is a synthetic process—that is, one in which substance is built up from simple raw materials, and inasmuch as the process takes place only in the presence of light it is one of photosynthesis.

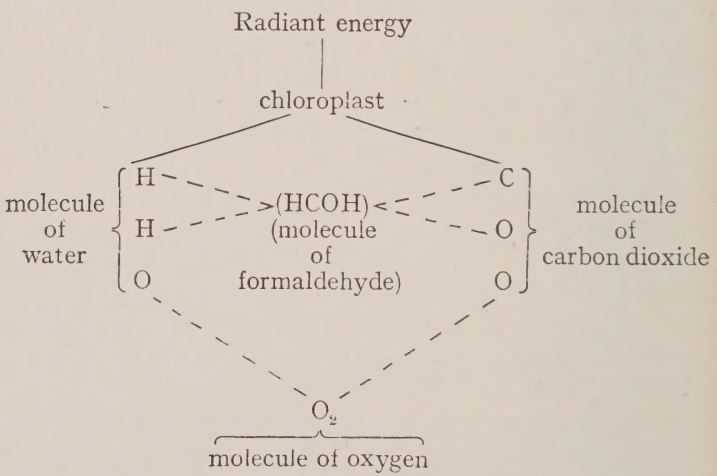
The assets which accrue to the plant as a result of photosynthesis are of two kinds : a gain of material and a gain of energy. The oxygen which is liberated is merely a by-product, for, although an adequate supply of oxygen is essential to the life of the green plant, so much is produced during photosynthesis that the plant can neither use nor retain more than a little of it and the excess escapes into the air. From the point of view of the world at large, however, the by-product is important ; for it helps in no small measure to make good the loss of oxygen from the atmosphere which goes on in every process of combustion.

The wheat plant alone, producing as it does a world crop containing some 70 million tons of carbohydrate, 'handles' each year about 114 million tons of carbon dioxide, and liberates to the atmosphere over 80 million tons of oxygen. The energy-value to the plant of the carbohydrate produced during photosynthesis may be computed on the basis of the amount of heat found by experiment to be liberated when a given amount of starch is caused to undergo combustion. The combustion of one ounce of starch liberates 116 calories and it is therefore only a matter of calculation to discover the energy-value in terms of calories of the carbohydrates of the world's wheat crop. The heat which would be produced by the combustion of the 70 million tons of carbohydrate would suffice to raise to boiling-point all the water of an ice-cold lake four miles long, four broad, and of an average depth of forty fathoms.

Yet even more important than the amount of energy which the plant secures to itself by the photosynthesis of carbo-

hydrates is the fact that the energy is, as it were, contained in small parcels—in the molecules of the synthesized carbohydrates—and may therefore be distributed in small or large doses to each and every part of the living plant.

How the transformation of carbon dioxide and water into carbohydrate is brought about is not fully known. It may be that the living chloroplasts deal with carbon dioxide and water molecules in pairs; that they, or other living parts of the cell, pick each molecule to pieces, extracting from each an atom of oxygen, and that the residual groups of atoms unite to form the compound of the composition HCOH, known as formaldehyde, thus:—



It may be further supposed that when six pairs of molecules have been operated on, and six molecules of formaldehyde have been produced, the latter condense, that is, unite to form one large molecule which is that of a sugar (dextrose):

$$6\,(HCOH) = C_6H_{12}O_6$$

On the other hand, it is possible that it is by other intermediate stages that carbohydrate is produced. It is not

even known with certainty in what form the carbohydrate produced during photosynthesis first makes its appearance in the green leaf. Because starch appears very soon it by no means follows that it is the first carbohydrate to be produced when the green leaf is exposed to sunlight. There are indeed strong grounds for believing that it is not.

Starch grains (Fig. 10, p. 37) are highly organized structures. They are composed of more than one kind of starch. Starches are of great chemical complexity. The general formula $C_6H_{10}O_5$ represents only the proportion of atoms of carbon, hydrogen, and oxygen in a starch molecule, and not the actual number of atoms in it. The number of atoms is far larger, and to express this fact the formula for starch is written $(C_6H_{10}O_5)_x$ where x is some whole number, probably not less than 200.

Physiological evidence against the claim that starch is the first carbohydrate-product of the green plant's synthetic operations is no less strong. There are not a few plants, (onions, and other Monocotyledons) in the leaves of which no starch appears after exposure to light. In them sugars are produced instead. So also sugars are to be found in increasing quantities in the sunlit green tissues of leaves which do produce starch. It may therefore be concluded that when a green cell brings about the decomposition of carbon dioxide and water it is a sugar which is first formed. The chemist would undoubtedly concur in this conclusion, for the molecules of sugar are of simple constitution compared with those of starch. The green leaf, however, may contain at any given moment several kinds of sugar, and it is hard to say which of these is the first product of photosynthesis. It may be cane sugar (sucrose), $C_{12}H_{22}O_{11}$. It may be dextrose, $C_6H_{12}O_6$.

Whatever the details of the photosynthetic process may prove to be there can be no doubt of the final result. Carbon constitutes nearly one-half of the dry weight of the green plant (Table II, p. 45). It occurs in manifold forms both in animals and plants. All this vast quantity of carbon which

circulates through the living world is the outcome and the measure of the photosynthetic activity of the green plant. But it is by no means the full measure. Of the organic compounds which occur in plants and animals, some—for example, carbohydrates and fats—contain only those elements, carbon, hydrogen, and oxygen, which are present in the raw materials used in the photosynthesis of carbohydrates. Other of them, however, including not a few which enter into the composition of protoplasm, are compounded of other elements as well. The proteins, for instance, several kinds of which are invariably present in protoplasm, contain even in their simplest forms nitrogen and sulphur as well as carbon, hydrogen, and oxygen, and the more complex proteins and protein derivatives include in their molecules phosphorus and potassium as well. These elements, no less than carbon, form threads of the chemical fabric of life, and are, as is carbon, won by the green plant from the outer world. As demonstrated by water cultures, they are obtained each from inorganic compounds—nitrates, phosphates, sulphates, and salts of potash—contained in the soil. The photosynthesis of carbohydrates, of which so much has been said, is therefore after all but one of several synthetic processes carried out by the green plant. The burden laid upon vegetation consists in bringing not carbon only but also nitrogen, sulphur, phosphorus, and potash, as well as other elements, into the vital circulation: transferring them from the simple, inorganic combinations in which these elements occur in the outer world into complex, organic materials which form parts of the living organism.

It is easier, however, to admire the variety of synthetic activities manifested by the green plant than to explain them. So little indeed is known of the chemical operations which result in the synthesis within the green plant, even of the simpler nitrogenous compounds, that it will be more profitable to state the broad facts than to describe the uncertain stages by which the several syntheses are supposed to take place; and even so to confine attention to the synthesis of nitro-

genous compounds, about which ignorance is a little less profound than it is of the processes whereby the other mineral elements are brought by the green plant from the outer world into organic combination.

Green plants, or at all events a large majority of them, may live and flourish with nitrates as their only source of nitrogen. Even though the free nitrogen and the trace of ammonia contained in the atmosphere be prevented from reaching it, the green plant grows as well as it does in ordinary air, provided that nitrates are present in the soil. The nitrate absorbed by the roots reaches the leaves. There it accumulates in plants kept in darkness ; but, so soon as a leaf is exposed to light, nitrates begin to disappear from it. The disappearance is dependent on the photosynthetic activity of the green cells ; for if variegated leaves are kept in darkness until their colourless and green cells have accumulated nitrates, exposure to light brings about a disappearance of nitrates only from the green and not from the colourless cells. Therefore the decomposition of nitrate—a preliminary stage in the synthesis of organic nitrogenous compounds—depends either directly or indirectly on the photosynthetic activity of the green leaf. Animals, so far as is known, lack altogether the power of carrying out this initial phase of nitrogen assimilation, and therefore it follows that the organic nitrogenous compounds contained in them owe their origin ultimately to the synthetic activity of the green plant.

The disappearance of nitrates from the illuminated green leaf is attended by the appearance in it of organic nitrogenous compounds in which nitrogen is combined with carbon, hydrogen, and oxygen. The compounds which arise as a result of this first stage of nitrogen assimilation belong to a numerous class known as amino-acids, which are characterized by the occurrence in them of one or more amino (NH_2) groups : as for example, amino-acetic acid or glycine :—

acetic acid = CH_3COOH

glycine = CH_2NH_2COOH

Many amino-acids, the composition of which is to be found in books on organic chemistry, have been isolated from plants. One of the most widespread, though certainly not one of the first synthesized, is asparagin, which is present in large quantities in asparagus and other plants. This and other amino-acid derivatives increase in quantity in plant tissues kept in darkness; but accumulation in this case is to be attributed not to a synthetic but rather to an analytic process; one in which some of the later-formed, more elaborate products of a previous nitrogen synthesis—as, for example, proteins—break down and yield amino-acids.

Amino-acids may be regarded as constituting a chemical half-way house between two stages in the synthesis of proteins. During the first stage amino-acids are produced, and during the second they are synthesized to proteins. Once the first phase of nitrogen assimilation has been accomplished, and amino-acids have been formed by the green tissues, any living cell, green or colourless, plant or animal, appears to be able—after changing them in suitable manner—to link up in due order different amino-acids—one with another to form a longer and longer molecular chain. When the chain-like molecule, made up of numerous linked groups of amino-acid residues, becomes very long it constitutes a protein.

The one set of compounds—the amino-acids—are of relatively simple molecular constitution, and are soluble and diffusible; the other set of compounds—the true proteins—are of extremely complex chemical and physical constitution, are indiffusible, and generally insoluble. Proteins themelves are of different orders of complexity. Some, the simpler proteins, constitute a floating reserve of nitrogenous food-material which may be used to repair and increase the protoplasmic machinery; others, the more complex, form an essential part of the machinery itself. Without them, and a constant reformation of them, protoplasm may neither exist nor persist.

Experimental evidence suggests that reserve proteins constitute indispensable raw material out of which protoplasm

elaborates the more complex vital proteins which form essential parts of both cytoplasm and nucleus. For example, seedlings of wheat and other plants, when they begin to germinate, contain both kinds of protein ; but as germination progresses the reserve proteins decrease in amount and the more complex vital proteins increase at their expense. Later, when photosynthesis begins, both kinds of proteins show an increase ; but if the germinated seeds and seedlings be kept in darkness so that photosynthesis is prevented, there comes a time when both reserve and vital proteins undergo a decrease. In the adverse conditions of prolonged darkness the protein-containing protoplasmic machinery breaks down, and, material for its repair becoming more and more deficient, the young plants starve and die. If, on the other hand, the seedlings emerge into the light, carbohydrate synthesis begins, and with it begin also the synthesis of amino-acids and their linkage to form reserve proteins, so that, with material available for repair, the vital mechanism is kept running and is enabled to augment itself : the plant grows and waxes strong.

The power possessed by the green plant of initiating the first phase of nitrogen assimilation confers on it a status unique, or all but unique, in the world. The green plant has a monopoly scarcely disputed by other organisms in the use of the world's stores of nitrate. All organisms lacking power to convert the nitrogen of nitrates into the amino form must needs depend, directly or indirectly, on the green plant no less for the nitrogen than for the carbon compounds which they must have : for the green plant alone has the art of the large-scale making of protein bricks without an extraneous supply of amino-acid straw. Nitrogen-fixing bacteria and possibly other micro-organisms may possess similar or even more profound powers; but their nitrogen syntheses are not on a scale large enough to supply the organic nitrogen-compounds required by the animal world.

The second phase of nitrogen synthesis—the formation of proteins from amino-acids—unlike the first, seems to present

no difficulty to any living cell—green or non-green, plant or animal. Given supplies of suitable amino-acids or of other organic nitrogenous substances from which the cell may form amino-acids, and given plenty of carbohydrate, every living cell is able to synthesize proteins.

To demonstrate the capacity fo non-green plant-cells to effect the synthesis of proteins from amino-acids, advantage is taken of the facts that large quantities of carbohydrates and of nitrogenous material are contained in bulbs and other storage organs, and that when the tissues of a plant are wounded they are stirred up to unwonted and great activity. Thus it is that when leek (*Allium porrum*) bulbs are cut up each into several pieces, the proteins of their tissues increase rapidly and considerably at the expense of the simpler organic nitrogenous compounds stored in them. A similar synthesis of proteins is also exhibited by hyacinths when, as is practised commercially in Holland, large bulbs are caused by ' slashing ' to give rise each to many daughter bulbs. So also protein synthesis from organic nitrogenous reserves occurs when in the early part of the year new potatoes are produced from old by planting the tubers in dark cellars.

The animal cell also possesses similar partial powers of protein synthesis ; like the non-green cells of plants it may synthesize proteins from suitable amino-cells. Yet animals, if they are to thrive, must be supplied with food containing proteins. The apparent contradiction may be reconciled. The surest and perhaps the only way of supplying an animal with the right kinds and due amounts of the amino-acids which it needs for the synthesis of the numerous and diverse proteins required by it is to give these compounds in protein form. By so doing the animal is left to pick the proteins to pieces, and from the amino-acid pieces to reconstruct its own proteins. The proteins contained in the food of animals are mostly insoluble and indiffusible, and cannot therefore be absorbed without change. The animal changes them by digestion, producing from the proteins soluble and diffusible

amino-acids. The latter are absorbed and reassembled in the living cells of the animal body, where they are pieced together in due order to form proteins.

Although wellnigh unique, the green plant is not absolutely without rival in respect of capacity for complete protein synthesis. Certain micro-organisms share with it the power of extracting nitrogen from inorganic sources and of sending it migrating through the living world. Among the many kinds of bacteria widely distributed throughout fertile soils, there is, in particular, one set, the nitrifying bacteria, consisting of two species working in partnership, which, in spite of obscurity of station, play a noteworthy part in the lives of plants and animals.

The nitrifying bacteria supply the green plant with nitrates, and, although devoid of chlorophyll, synthesize organic carbon- and nitrogen-compounds from simple inorganic raw materials. What supplies the place of sunlight as a source of energy for the process must be considered presently (p. 148); here it is only a question of how the nitrifying organisms live their lives. Others' meat is their poison. The nitrifying bacteria cease activity if they are in contact with more than a trace of organic matter. They only begin it when they have access to supplies of ammonia, carbon dioxide in the form of carbonates, water, and essential mineral substances.

It is not difficult to show that the micro-flora of the soil does indeed bring about nitrification. A long glass tube filled with arable soil contains large numbers of nitrifying as well as other kinds of bacteria. If weak manure water, containing ammonia, but poor in organic nitrogen-compounds, is caused to percolate slowly through the tube, the deodorized liquid which escapes lacks ammonia and contains nitrates. Nitrates produced in this natural way served Napoleon for gunpowder-making when, owing to our blockade, the importation of saltpetre into France was stopped. The production of nitrate by the agency of soil bacteria may be kept going for a long time, but anything which interferes with the vital activity of the

bacteria brings nitrification to an end; for example, if chloroform be added to the soil the bacteria are anaesthetized and lose power of nitrification. On the other hand, soil partially sterilized, as, for example, by heating it to about 150° F., gains added power of nitrification, due perhaps to the destruction of rival bacteria which in unheated soil undo the work of nitrification by converting nitrates into ammonia. Whether this be the explanation or no, it is certain that the soil contains denitrifying as well as nitrifying organisms. The smell of ammonia from a manure heap testifies to their existence and the form of their activity.

As a result of the activity of the nitrifying organisms, ammonia is oxidized by one of the partners to nitrite (NO_2), and nitrite is oxidized by the other to nitrate (NO_3). Simultaneously with the production of nitrate the nitrifying organisms increase and multiply, and increase and multiplication are attended by augmentation in their bodies of organic carbon- and nitrogen-containing compounds. Both carbon and nitrogen must have been obtained from the outer world, the former presumably from carbon dioxide, and the latter from ammonia in the case of the nitrite-forming and from nitrite in that of the nitrate-forming bacteria.

Here the long story of the acquisition, assembling, and chemical transformation of raw materials by the green plant comes to an end. A sketch rather than a story: for more knowledge must be discovered before the tale may be well and truly told. Yet as a story should, it tells of great enterprises and hints at deep mysteries to be unravelled in a sequel yet to be composed. The green plant, the one real capitalist of the world, has now amassed a wealth of carbohydrate and protein food-material. It remains to discover what the plant is going to do with it.

V

The mobilization of food-materials. Physical and chemical properties of carbohydrates and proteins. Diffusion. Osmosis: osmotic pressure. Colloids and non-colloids: the colloidal state. Enzymes and the part they play in mobilization. The conducting system of the root and stem.

When at sunrise on a summer day a ray of light falls upon a green leaf the plant is quickened into instant activity. Throughout the hours of sunlight the formation of sugar and of organic nitrogenous food-materials goes on, until towards evening the synthetic processes are slowed down and arrested automatically, either by the accumulation of the products of manufacture or by the shutting off of power as the sun declines. Yet notwithstanding the daily renewal of photo-synthesis, neither carbohydrates nor nitrogenous food-materials go on accumulating indefinitely in the leaf. The starch formed to-day in the green cells of the leaf will have disappeared by to-morrow, leaving the cells in which it was formed free to accept delivery of a fresh consignment. The sugars and the synthetic nitrogen products also disappear from the leaves in which they were formed. As levies of recruits remain in depots, awaiting mobilization until drafted for active service, so each day's recruitments of synthesized food-materials remain for a time in the cells in which they were formed before they too are mobilized for active service. A molecule of sugar brought into existence on a summer day by the assimilatory activity of the green leaf may before autumn sets in be found interned in one form or another in a cell of the stem or root—a migration which, if the plant be one of the great trees, may involve a journey of a hundred yards or more. Before next spring has merged in summer the

same sugar molecule may be back again in a young bud near its place of birth in the leaf.

The sojourn of the food-materials in the plant that made them may be brief or long, and the changes which they undergo may be many or few and great or small. But before the alternative fates which await them befall the food-materials they must go out to meet them. Locked up in the leaf the food-materials are as useless to other parts of the plant as is hoarded gold to any member of the community other than the miser. To serve the plant's needs the food-materials must be accessible to every living cell of root and stem, leaf and flower.

Understanding of the nature of the mobilization which the food-materials undergo, and the manner of their migration, needs inquiry into the physical and chemical properties of the materials themselves and a survey of the routes by which they pass.

Carbohydrates, of which many kinds occur in plants, constitute a series of related organic compounds of ascending complexity. The simplest are the sugars; the more complex are the starches; and the most complex are the celluloses, some of which enter into the composition of the cell-walls of plants. Sugars, starches, and celluloses are grouped together as carbohydrates because their several molecules are all built on the same fundamental plan. They all consist of carbon, hydrogen, and oxygen, and in a molecule of any of them the proportion of hydrogen to oxygen atoms is that of the hydrogen and oxygen of water (H_2O)—two to one. All carbohydrates therefore may be represented by the general formula: $C_mH_{2n}O_n$. Throughout the series, from simplest sugars to most complex celluloses, the numerical value of m and n—that is, the number of atoms in the molecule—increases from a relatively low figure to a very high one. In one of the simpler sugars —dextrose—m is 6 and so is n; hence the general formula $C_mH_{2n}O_n$ becomes $C_6H_{12}O_6$. In cane sugar m is 12 and n is 11, so that its formula is $C_{12}H_{22}O_{11}$. In starches and celluloses m is some very large multiple of 6, and n a very large

multiple of 5, and so the general formula becomes $(C_6H_{10}O_5)_x$, where x is perhaps 200 or more. A molecule of a starch may therefore be represented by some such formula as $C_{1200}H_{2000}O_{1000}$; and even so it is less complex than is a molecule of cellulose.

The essential similarity in chemical constitution of sugars, starches, and celluloses is manifested by the readiness with which higher carbohydrates may be caused by simple chemical means to give rise to sugars. Dextrose—or, as it is known in commerce, glucose—is produced industrially by treating the starchy residues of plants with acid. Any one who will sow date-seed may trace step by step by means of the microscope the disappearance of the thick cellulosic deposits on the walls of the endosperm, and may ascertain that, following on the disappearance, simpler carbohydrates—as, for example, sugars—make their appearance in the embryo. The green plant possesses, indeed, remarkable power of transforming carbohydrates of one form into another. If a green leaf kept in darkness till all starch has disappeared from its cells be floated on a weak solution of a sugar it absorbs so much, and transforms sugar into starch so fast, that the leaf, although no light has reached it, turns a blue-black colour when treated with iodine. A potato tuber contains large quantities of starch and so little sugar that it has no sweetness, yet, if potatoes be improperly stored, starch may be changed to sugar and the tuber may become sweet during a spell of frosty weather. If the frost be severe the potatoes are killed, turn brown, and rot; but if the temperature of the tubers does not fall below 4° C. they turn sweet, but are not killed. When the temperature rises again sugar disappears and starch appears in its place. Thus may a plant swing a carbohydrate backward and forward from one form to another.

The uniformity of plan of carbohydrate molecular construction is shown also by the readiness with which the more complex sugars may be transformed into simpler sugars. Sucrose (cane sugar), $C_{12}H_{22}O_{11}$, boiled with water gives rise to

the two sugars, dextrose and laevulose (grape sugar), each of which is represented by the same formula, $C_6H_{12}O_6$. The change produced by boiling cane sugar with water may be followed by means of the polarimeter—an instrument which may be used to determine whether a given substance produces rotation of the plane of a beam of polarized light passed through it. If the light be rotated the substance is said to be optically active, and if not, optically inactive.

The polarimeter may be employed also to compare the strengths of solutions of the same optically active substance; for rotation is caused by the molecules of optically active substances, and within limits the greater the number of molecules in a given volume of water the greater is the rotation. Advantage is taken of this method of measurement where beet sugar is grown on co-operative lines. Thereby the refiner is in a position to pay the farmer as soon as the crop is lifted and its weight determined. A few pieces bored from a series of beet roots, extracted with water and examined by the polarimeter, permit of the refiner making a close estimate of the amount of cane sugar contained in the crop, and from percentage of sugar and yield of crop he calculates its value, and the farmer—for once a happy man—may be paid even before the 'roots' are carted to the factory. Furthermore, when, as happens with cane sugar boiled with water, an optically active substance is destroyed and other optically active substances (dextrose and laevulose) are produced, it is possible to determine by means of the polarimeter the rate at which the change takes place. For a molecule of cane sugar in solution has its own definite rotatory power, and so has the molecule of any other optically active substance. Cane sugar rotates the plane of a beam of polarized light to the right (clock-wise); so does dextrose—hence the right-handed implication of the name. Laevulose, however, is a sinister—that is, a left-handed—sugar. It brings about an anti-clock-wise rotation, and the 'left-handedness' of a laevulose molecule is greater than the 'right-handedness' of a sucrose or a dextrose

molecule. So soon as laevulose has been formed by boiling a solution of sucrose it begins to produce its left-handed effect. The solution becomes less dextro-rotatory than before, and, as the amount of laevulose increases, rotation to the right becomes less and less, until finally the mixture sucrose, dextrose, and laevulose in the solution shows itself in the polarimeter as left-handed: the plane of polarized light is now rotated anti-clock-wise. Owing to the reversal which occurs during the change of sucrose to dextrose and laevulose it is customary to speak of the inversion of sucrose.

The inversion of cane sugar may be regarded as being brought about by the union, in pairs, of sugar and water molecules. It is therefore a hydrolytic change—a hydrolysis. When water and sucrose molecules have entered into association with one another the complex they form does not endure, but is resolved into a molecule of dextrose and one of laevulose thus:

$$C_{12}H_{22}O_{11} + H_2O = \left\{ \begin{matrix} C_{12}H_{22}O_{11} \\ H_2O \end{matrix} \right\} = C_6H_{12}O_6 + C_6H_{12}O_6$$

sucrose water sucrose-water complex dextrose laevulose.

The sucrose-water molecular complex becomes cloven into two halves, and the change is therefore described as a clastic change. Inversion of cane sugar involves therefore a hydrolytic and a clastic operation. If in other circumstances the reaction were to go the other way, and one molecule of sucrose were formed from one of dextrose and one of laevulose, the equation might be written:

$$\begin{matrix} \text{dextrose} \\ C_6H_{12}O_6 \\ C_6H_{12}O_6 \\ \text{laevulose} \end{matrix} = \underset{\text{sucrose}}{C_{12}H_{22}O_{11}} + \underset{\text{water}}{H_2O}$$

and it is evident that, for the change to come about, the two atoms of hydrogen and the one of oxygen contained in the molecule of water which is withdrawn from the sugars must be abstracted so delicately that there is but little interference

with the grouping of the remnants of the dextrose and laevulose molecules, and so it happens that the two remnants unite or condense to form one molecule of sucrose. Because of the chemical relations revealed in this and similar reactions such sugars as dextrose and laevulose are described as monosaccharides, and such sugars as sucrose as di-saccharides.

For similar reasons starches and celluloses are classed together as polysaccharides. Like the sugars they, or at least many of them, may be caused to undergo hydrolytic and clastic change similar in essentials to, but more far-reaching in extent than, that sustained by sucrose when boiled with water. In the hydrolytic and clastic changes which may be brought about in starches and celluloses one molecule gives rise, not to two, but to more than two molecules of one or more sugars : hence the term polysaccharides. When, for example, starch is treated with water and mineral acid, the numerous $C_6H_{10}O_5$ groups (p. 93) of which the molecule is composed are, as it were, taken one by one, and united each with a molecule of water to form a molecule of dextrose. When, however, starch is acted on by less drastic reagents, the product of change may be not dextrose but the di-saccharide maltose (malt sugar) of the same formula as sucrose ($C_{12}H_{22}O_{11}$). In this case the molecular lock-picking done by the water molecule may be represented thus :

$$\left.\begin{matrix} C_6H_{10}O_5 \\ C_6H_{10}O_5 \\ C_6H_{10}O_5 \\ C_6H_{10}O_5 \end{matrix}\right\rangle + H_2O = C_{12}H_{22}O_{11}$$

and so on.

The residual ($C_6H_{10}O_5$) groups condense together and give rise to intermediate products—e. g. dextrins—which, undergoing a like hydrolytic change, ultimately yield sugar molecules, till finally only maltose and an unhydrolysable residue of the starch grains are left.

The progressive chemical complexity of sugars, starches, and celluloses is reflected also in their physical behaviour. The

sugars are soluble. They form true solutions with water. The starches, though they swell with water to form a sticky paste, do not form true solutions. Boiled for a long time with water, starch becomes distributed through the liquid medium and gives rise to an opalescent, uniform mixture of water and starch; but it is not a true solution. Celluloses are quite insoluble in water, and though, like starch, they imbibe water and swell, yet they retain their solid form even when they have taken up all they can.

Sugars are diffusible, starches and celluloses are not. As a scent diffuses itself through still air, so sugar in solution becomes diffused throughout the water in which it is dissolved. The diffusion of sugar or other diffusible substance is rendered possible by the fact that in solution the aggregate of molecules which make the solid breaks down and liberates free molecules, which distribute themselves among the free molecules of water. Molecules are never still. They are always making excursions to and fro, and as a result of the multiplicity of these movements water and sugar molecules come ultimately to be distributed uniformly throughout the medium in which they move. Diffusion, dependent as it is on the movements of molecules, is a slow process. The quickness with which a lump of sugar sweetens even an unstirred cup of tea is due to the assistance given by slight movements of water and cup to the mass movement and diffusion of water and sugar.

To show how slow is diffusion when it is unaided by disturbance of the medium, the process may be caused to take place in circumstances which preclude mass movements. A narrow cylindrical glass jar (Fig. 19) is filled with a solution of gelatine strong enough to set at room temperature. Mixed with the gelatine whilst it is warm, and before it is poured into the jar, is a small quantity of phenyl phthalein, a substance which gives a rose colour with alkalis. When the gelatine is set the glass jar containing it is fixed in a retort stand, and inverted over a strong solution of potash contained in a vessel stand-

ing on a steady table. The rate of diffusion of the potash may be measured day by day by the progress up the tube of the rose colour produced by the interaction of phenyl phthalein and potash. It is evident that mobility due to diffusion cannot be left out of account when that of the food-materials of plants is considered ; but it is no less evident that diffusion alone would make the transportation of sugar from leaf to root of a great tree a very slow passage.

Starch and cellulose possess the opposite property. They are indiffusible. Even though the fine particles made up of starch and imbibed water which give opalescence to a starch solution may, by reason of their minuteness, possess some power of movement, the movement is not free like that of molecules. The difference between sugar and starch in this respect may be demonstrated by the use of a parchment membrane like that used for jam-covers, made into a tube closed at one end. If the parchment tube be nearly filled with a sugar solution and immersed in water, sugar diffuses out just as it would were no parchment there, and very soon the sweetness of the water outside betrays the escape of sugar molecules from the solution inside the parchment tube. On the other hand, an opalescent starch solution put into the parchment tube remains there. So absolute is the difference in behaviour that a parchment tube may be used to separate starch and sugar from a solution containing both. To separate them completely, however, requires the periodical renewal of the water outside the parchment tube : for if it were not renewed, as diffusion went on the water outside would come to have the same concentration of sugar as that in the water within the parchment tube. When that happened the rate of diffusion in the one direction would be equal to that in the other, and therefore some sugar would remain mixed with the starch. By renewing the water outside the tube outward diffusion goes on again until equilibrium is once again reached, and so with frequent renewal of water the last molecules of sugar may be removed from the mixture.

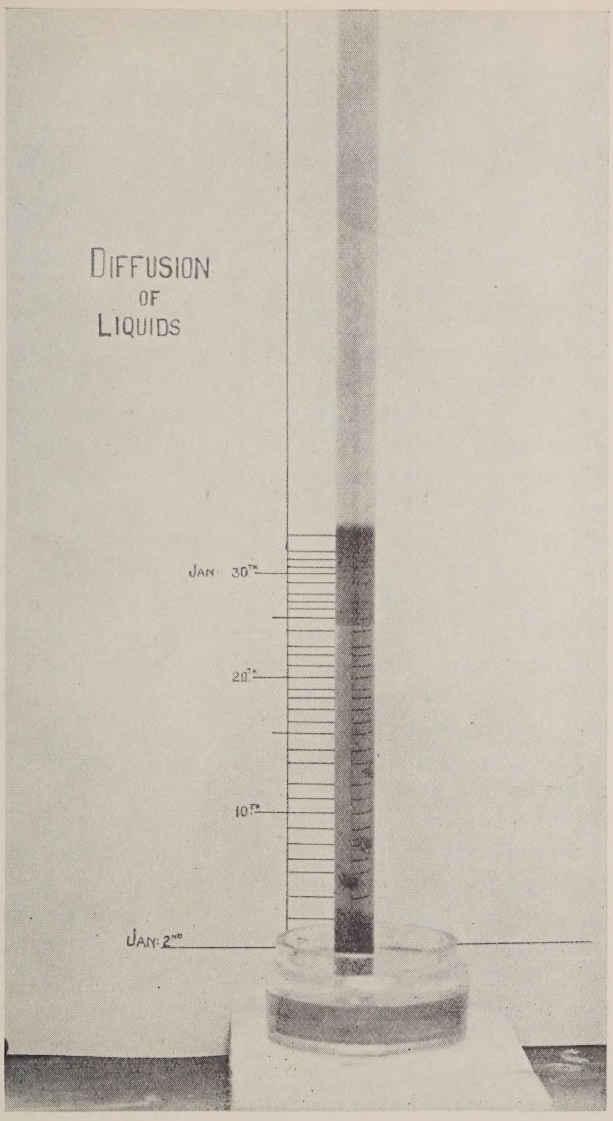


FIG. 19. Record of the rate of diffusion of potash in solution (height reached by potash in the experiment = $7\frac{1}{2}$ in. in 32 days).

The addition to the parchment tube of a cork bearing two glass tubes—a short one for filling and a long narrow one for recording—fitted into the open end (Fig. 20) permits of closer investigation of the behaviour of sugar or similar diffusible substance in solution. The parchment apparatus is held in position over a vessel containing water, and whilst a strong solution of sugar containing a little soluble, diffusible dye is poured through the wide filling-tube which just, and only just, reaches to the bottom of the cork in which it fits, the parchment tube is lowered into the water. When the parchment tube is completely full the filling-tube is closed, and more water is poured into the outer vessel until it is nearly at the level of the cork. In a short time the parchment wall becomes taut and water begins to rise in the recording tube, and goes on rising until, after a day or so, it may have reached a height of several yards. Then, either suddenly with a run due to the heavy water column finding a weak place in the apparatus and breaking it, or slowly, the water column falls to its original level. In the meantime the sweetness of the water shows that sugar has passed into the outer vessel, and its colour demonstrates that the dye has passed out also. The rising water column shows that water has passed into the inner vessel. It is no less evident that work has been done: water has been lifted to no inconsiderable height. To hold up this water column the sugar solution must exert pressure. Substances which, like sugar, are able in similar circumstances to exert pressure are known as osmotic substances, and the pressure which they exert is known as osmotic pressure. As a result of that pressure, water, owing to the fact that the membrane opposes no barrier to its diffusion, passes molecule by molecule from the outer vessel into the parchment tube.

The final fall of the water column is due to the diffusion outwards of sugar. Parchment membrane is permeable to sugar molecules as well as to those of water. A sugar molecule which passes into the outer vessel exerts osmotic pressure

just as do the molecules within the tube. As, therefore, sugar accumulates outside, its osmotic pressure comes more and more to balance that of the sugar in solution within the tube. With continued dialysis of sugar from within outward, the osmotic pressure in the tube grows less and that outside more. When they balance there is nothing to hold up the water column and so down it comes. If the molecules of sugar did not diffuse out from the parchment tube—in other words, if parchment were impermeable to sugar—it is evident that water would rise to a much greater height, and that the height to which it ultimately rose would give a measure of the osmotic pressure exerted by a sugar solution of known strength — that poured into the parchment tube. Membranes of such a kind, permeable to water but not to certain other diffusible substances, and hence called semi-permeable membranes, have been discovered and made, and by their use the osmotic pressures of different substances which occur in plants have been measured. These measurements have enriched physical knowledge, have permitted the discovery of the laws which govern osmosis, and, what is of

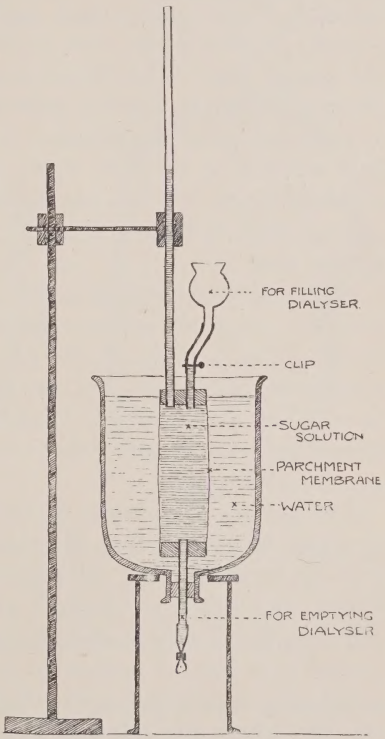


FIG. 20.
Osmotic apparatus as described in text.

no less importance to the plant physiologist, have shown that the pressures exerted by sugars, organic and inorganic acids, and other osmotic substances dissolved in the cell-sap are astonishingly great. The cell-sap of the beet root, which contains much cane sugar, is capable of setting up an osmotic pressure equal to 20 atmospheres, that is, 300 pounds per square inch. The pressure exerted by the osmotic substances present in actively growing cells is even greater, and in extreme cases—for example, in some desert plants, which find water hard to come by in the dry soil and difficult to withhold from the hot sun—it may amount to 100 atmospheres, that is, three-quarters of a ton (1,500 pounds) to the square inch.

In the light of these facts the vegetable cell acquires a new interest. It is an osmotic apparatus of remarkable power, more subtly and variously planned than the parchment-membrane apparatus, but nevertheless working on similar lines. The living boundary walls of the cell constitute the osmotic membrane, and the cell-sap a reservoir of osmotic substances.

The osmotic membrane of the vegetable cell is, however, as might be expected, more complex than any artificial semi-permeable membrane. It consists of several parts, each of which has different osmotic properties: the cell-wall of cellulose which may perhaps be likened to a parchment membrane, and, like it, permeable to water and other diffusible substances; and the surface layers of cytoplasm of which the outer lines the cell-wall and the inner bounds the space or vacuole containing the cell-sap.

These, the inner and outer plasmatic membranes (Fig. 21), composed of living cytoplasm, possess the property of semi-permeability, so that whilst permeable to molecules of water, and, it may be, to some diffusible substances, they are impermeable to other diffusible substances. Thanks to their properties a substance, though capable of diffusing across the cell-wall, may be prevented from entering or leaving the cell.

A slice of red sugar-beet suspended in water allows of no escape of either pigment or sugar. But if the water be heated there comes a moment when the cells are killed, and the plasmatic membranes are destroyed. At that moment sugar and pigment begin to diffuse out through the permeable cellulosic cell-wall.

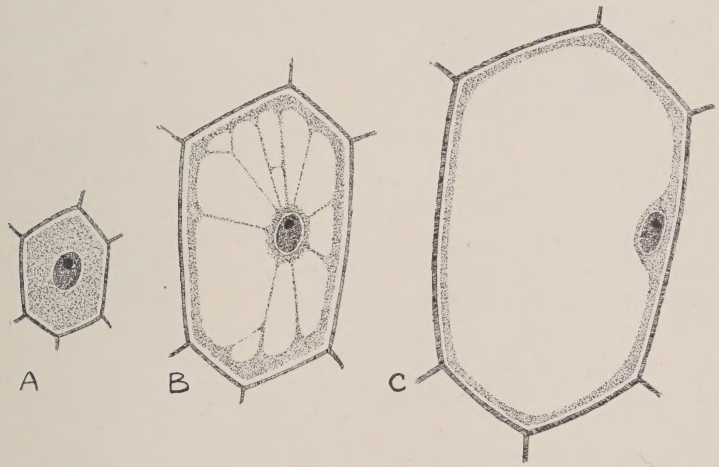


FIG. 21. Stages in development of a plant cell. A, young cell with central nucleus and cytoplasm; B, older cell showing vacuolated cytoplasm C, mature cell with persisting nucleus, the cytoplasm reduced to a peripheral layer bounding the large vacuole containing cell-sap: the outer and inner faces of the cytoplasmic layer constitute the plasmatic membranes.

The osmotic system formed by membranes in contact on either side with water ensures that the living cell, the sap of which contains osmotic substances, shall be able to absorb water whenever it is available, and ensures also that water absorbed by one cell shall be distributed to all. For consider two neighbouring cells containing equal amounts of the same osmotic substances. One, for example a root-hair cell (Fig. 14, R), is in touch with water in the soil. If the osmotic pressure of the root-hair cell is greater than that of the mineral substances in the soil solution, absorption of water takes

place. The root-hair cell increases in volume, its cell-walls are stretched and kept stretched by osmotic pressure. Pressure engaged in one way cannot at the same time be used in another, and hence water contained in a fully distended, turgid cell may easily pass from it to a neighbouring cell containing osmotic substances and not yet fully supplied with water. The root-hair cell, however, losing water to its neighbour, decreases in volume, and relaxes its walls, and the osmotic substances are free again to exercise osmotic pressure in the absorption of water from the soil: thus may each and every cell of the plant gain a share of the water absorbed by the root. Stretched and made taut by water absorbed osmotically, the fully distended, turgid cell has no power either to absorb water or to prevent withdrawal by any neighbouring cell capable of exerting an osmotic pressure. For in the turgid state the osmotic pressure of a cell is wholly engaged in keeping the walls on the stretch.

A turgid cell and tissue composed of turgid cells exhibit the supple firmness so characteristic of living healthy plants. Deprived of water, cells become plasmolysed (Fig. 22), that is, they decrease in volume, their walls lose rigidity, and the cell or tissue wilts and becomes flabby. Slices of cucumber freshly cut are turgid and tough, and incidentally indigestible; covered with a layer of osmotic substance, salt, for example, they lose water and become soft, and, it may be added, less indigestible. It is in a large measure to the turgidity of their cells that young plants owe their powers of retaining their shape and of opposing resistance to constraint from without. Seedlings force their way through hard ground, hold themselves erect, and spread out their leaves before they have developed more than a very weak woody skeleton, and the roots of plants such as thistles growing vigorously in hot countries may upon occasion lift and twist railway lines beneath which they happen to be growing.

The osmotic system of the plant has manifest bearings on the manner of transport of food-materials. Its mode of

working suggests that the transport-system of plants is an hydraulic one, in the sense that all the transport is effected by water and that all the food-materials which are translocated travel in soluble and diffusible form. Starch—solid, granular, and insoluble—is well enough for storage, but it is

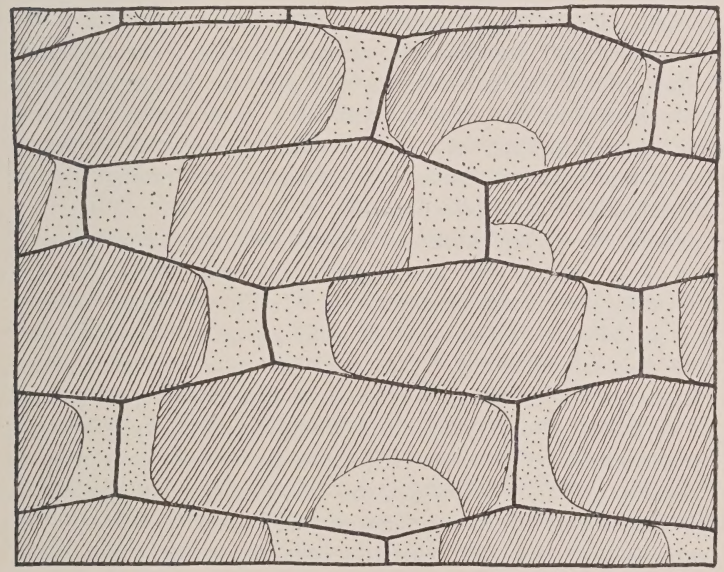


FIG. 22. Diagram of plasmolysed cells of the lower epidermis of a leaf of *Tradescantia discolor* after 15 min. immersion in a 1 % solution of potassium nitrate. Black lines indicate cell-walls—shaded tracts, the cytoplasm, which may be seen contracting away from the cell-wall owing to exosmosis of water from the vacuole.

as soluble, diffusible sugar that the carbohydrates synthesized in the green leaf reach the rest of the plant. So also is it with the nitrogenous food-materials: if they are to be transported from one part of the plant to another it can scarcely be in the form of indiffusible proteins, but rather as soluble and diffusible amino-acids.

Substances which, whilst not reacting chemically with

water, exhibit a change of state in its presence may be divided into two classes. One, the crystalloids, includes substances which, like sugar, form with water true and diffusible solutions. The other, the colloids, comprises substances which, like starches, celluloses, and proteins, are characterized by lack of power to form with water true solutions; some of them, it is true, possess properties which approach those of crystalloids, forming, for example, clear solutions with water; but nevertheless even they may be distinguished by their behaviour from true crystalloids. As, however, one and the same substance may exist in either form it is usual to speak not of crystalloids and colloids, but rather of the crystalloidal and colloidal state.

There are several kinds of colloids. Some, the emulsoids, of which milk provides an example, consist of liquid particles of minute dimensions suspended in a liquid medium. Others, the suspensoids, occur as fine, solid particles uniformly dispersed throughout the liquid medium, and in such minute state of division that they remain in suspension and do not settle down. Others again, for example starch and probably clay, owing to their power of imbibing water, form with it colloidal solutions in which the colloid occurs dispersed in the liquid medium in the form of minute semi-solid particles composed of the solid with its imbibed water. Yet other colloidal substances, blotting-paper (cellulose), &c., though they may retain solid form, show their colloidal properties by imbibing and swelling with water.

The dispersal of the particles throughout the liquid of a colloidal solution is not to be ascribed solely to the minuteness of the particles. Each minute, suspended mass carries an electrical charge of uniform sign—plus or minus. Particles similarly charged repel one another, and so, as a jostling crowd takes an interminable time to make its way through an open door, the constantly and mutually repelled particles are kept on the bound and remain suspended and dispersed in the watery medium. They may be made, however, to

settle down by bringing about the neutralization of the electrical charge which the particles bear. The addition of another colloid with oppositely charged particles may cause the settlement or precipitation of a colloid: or it may be effected by the addition of a crystalloid which, when dissolved in water, undergoes molecular dissociation with the liberation of ions carrying a charge of opposite sign to that of the colloid. The behaviour of certain proteins in the presence of sulphate of ammonia provides an illustration of the latter method. Thus albumen, one of the proteins contained in the white of egg, dissolves in water to form a clear, albeit indiffusible solution; but if the solution be saturated with ammonium sulphate, although neither the salt nor the protein undergoes permanent chemical change, the albumen is precipitated.

Any one who boils an egg may satisfy himself that the colloidal state of proteins may be permanently changed by heat. The white of the egg, which consists of water with sundry proteins, chiefly albumins and globulins, is coagulated by heat. Another illustration of a less drastic modification of the colloidal state by neutralization of the electrical charge carried by suspended particles is provided by the behaviour of a suspension of clay in water. Clay shaken up with water leaves, after the heavy particles have settled down, an opalescent colloidal solution, through which the extremely minute clay particles imbibed with water are dispersed. In this state it may remain for weeks. The addition of lime-water, however, soon removes the milkiness. The electrical charges of opposite sign carried by clay particles and by the calcium (Ca) ions of lime-water neutralize one another. The clay particles no longer repel, but cohere with one another. Flocculent aggregates of the watery clay particles are formed and rapidly settle down. Thus it is that by liming heavy clay soil its stickiness is removed, and land which previously was difficult to work, plastering tools and boots with greasy clods, and requiring four horses for its ploughing, becomes

for a time easier to work, losing its stickiness, and needing but a pair of horses for ploughing. The salts of sea-water produce an effect similar to that of lime. River-water carrying clay particles in suspension, where it meets the sea drops its load and forms a delta.

Heat, if fierce enough, destroys once and for all the colloidal state of clay. Instead of becoming puddled during rain and caking brick-hard in dry weather, a clay soil, if thoroughly burned, breaks down to a powdery state very kindly to the cultivator.

Clay and certain other colloids, including many which occur in the plant, exhibit another no less important property—that of adsorption. Adsorption may be illustrated by dipping strips of blotting-paper each into one of a series of dyes in solution. With some dyes the blotting-paper takes no stain, but with others it stains deeply. In the latter cases the colloidal particles of the dye are adsorbed by the colloidal surface of the blotting-paper, probably because they carry the opposite electrical charge to that carried by the closely bound particles of the blotting-paper. Thus, by virtue of its colloidal properties the paper picks out and accumulates so much of the dye that it becomes of a colour deeper than that of the solution into which it dips : colloidal paper and colloidal dye form together an adsorption compound. Adsorption may be illustrated also by pouring into a long glass tube packed with soil a dilute solution of sulphate of ammonia. The issuing liquid contains none of that substance. The sulphate of ammonia has been adsorbed by the colloidal particles of the soil. A solution of nitrate of soda, on the other hand, passes unchanged through the tube : hence the loss of soil-nitrates by the leaching action of winter rains, described on p. 21.

Power of adsorption is undoubtedly exerted by the colloidal contents of plants. It is shown by the fact that different parts of a cell take up dyes differently, and, in consequence, by using more than one dye it is possible so to stain the cells of plants that their several parts may be distinguished from

one another—nucleus of one colour, cytoplasm of another, and cell-walls of yet another; for even in dead tissues each of these complex colloids has its own distinctive power of adsorption.

Facts such as these make it not difficult to suppose that adsorption exercised by the living protoplasm may give a cell the means of picking out and holding for use food-materials or other substances which may reach it. Neither is it hard to believe that with such a changing and complex thing as protoplasm the power of adsorption may vary with its changing state, so that one and the same substance may now be held firmly by adsorption, and now, held not at all, be free to be moved on by water-transport to some other cell that needs and may adsorb it. Such power of selective adsorption with power to forgo it would suit the plant very well. In the future, books on the life of plants will devote the majority of their pages to the exposition of the colloidal properties of the higher carbohydrates, proteins, chlorophyll, and protoplasm, but at present this branch of knowledge, great as has been its growth, has not been applied sufficiently to biology to provide more than suggestive hints of the explanation of the behaviour of the living cell with respect to power of absorbing or excreting, that is, taking in or giving out this or that substance.

Nevertheless, it is clear that the colloidal properties of starches and proteins must be kept in mind throughout any study of the mobilization of food-materials. No more than the colloid gelatine of the experiment described on p. 97 interferes with the diffusion of potash need the colloidal protoplasm interfere with the osmosis of water or other diffusible substance into or out of the cell-sap; and as a semi-permeable membrane may allow the osmosis of water but prevent the passage across it of certain osmotic substances, so may cytoplasm; but whereas the semi-permeability of an artificial membrane is fixed, that of the natural living membrane is not. Though at one time the plasmatic

membrane of a cell may prevent ingress or egress of a soluble, diffusible substance, at another the membrane may permit it. The cells of a young beet root are rich in cane sugar, and contain little or no laevulose ; yet beet kept long in storage contains much laevulose. It would appear that during storage the permeability of the protoplasm changes, and that agents of the cell capable of inverting cane sugar, but previously kept out of touch with it, are now brought into contact with and hydrolyse the sugar to laevulose and dextrose. So also by virtue of its colloidal properties the cell, minute though it may be, may behave as though it were a factory or a city of factories in the parts of which work of diverse and even opposite kinds is carried on ; here a house is being built, and there one is undergoing demolition ; in one part, food is being manufactured, in another, dispatched, and in others is being accepted by a household. Imagine the colloidal cytoplasm of a vegetable cell to be fashioned microscopically after the manner of a honeycomb, each compartment separated from others not by dead wax, but by living cytoplasm. By adjustment of the powers of permeability and of adsorption of the different cytoplasmic partitions, one and the same cell might at the same time be building and demolishing, manufacturing food-material, dispatching and absorbing it.

Study of the physical properties of carbohydrates and proteins has shown that of the alternative forms in which each of these classes of substance occur in the plant one is suitable for storage, the other for transport. It has also been shown that the plant converts the one form into the other, changing, for example, starch into sugar and back again to starch. The nature and agents of this and similar changes need therefore to be discovered.

Changes such as those involved in the formation of sugar from starch, or in the inversion of sucrose, are brought about outside the living plant or animal only by drastic reagents. To convert any large quantity of sucrose into dextrose and laevulose, solutions must be boiled long and vigorously, and to

produce glucose from starch requires the use of both heat and powerful reagents. Yet the plant effects these and a multitude of similar operations quickly and without resort to high temperatures. A hint of the method by which the plant brings about many of its chemical changes may be got from the fact that the addition of a trace of a mineral acid—e.g. hydrochloric acid—speeds up in remarkable manner the inversion of cane sugar by boiling water. It might be supposed that the acid, which is a powerful reagent, produces its accelerating effect by some chemical action. For example, a drop of hydrochloric acid added to chalk sets up vigorous effervescence and gives rise to the formation of calcium chloride, thus :—

$$2HCl + CaCO_3 = CaCl_2 + H_2O + CO_2$$

So it might be imagined that the acid enters into permanent combination with the sugar. In point of fact it does not. A mere trace suffices to accelerate the inversion of sucrose, and the acid is not decomposed in the process. Its role is not to initiate, but to speed up the change. To express this fact the acid is said to act catalytically—letting loose, but not entering permanently into the chemical change.

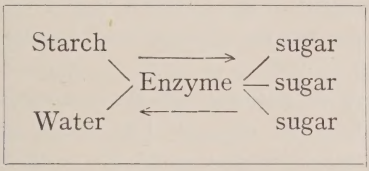
Bodies with similar properties occur in plants. Each is an activator, not of chemical change in general, but of a particular chemical change. These catalytic agents of the plant are known as enzymes, and their presence may be discovered wherever changes of food-materials are occurring. For example, crushed beet root yields, when treated with alcohol, a precipitate which dissolves in water to form a clear colloidal solution possessed of remarkable powers of speeding up the inversion of sucrose. The catalyst is known as invertase. Extremely little of it suffices to hydrolyse large quantities of sucrose. The solution of sugar to which it has been added must not be heated, however ; for enzymes, like proteins, are so sensitive to heat that they are ' killed ' well below the boiling-point of water, and generally at temperatures not many degrees higher than those at which the plant itself is destroyed.

Industry, long before anything was known of enzymes, had been accustomed to make use of them. The maltster, for a hundred years and more, has caused barley to work in his interest in converting starch to sugar, and, having got that work done, has caused another plant, yeast, to convert sugar into alcohol. Both operations are brought about by enzymes. In the malting of barley, so soon as the grain has sprouted the temperature of the malt-house floor is raised to a point which just suffices to kill the grain. The enzyme or enzymes (diastases), for there are more than one, are not killed, but remain to speed up the hydrolysis of starch to malt sugar.

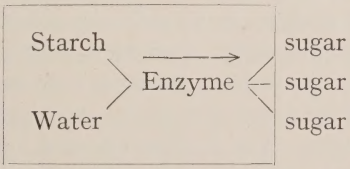
The diastases may be extracted by the method used for invertase, and may be made to do the work of accelerating the conversion of starch to sugar in a test-tube. The solution of diastases is not a true solution. Placed in a parchment tube diastase does not diffuse into the water outside. Similarly it may be shown that enzymes generally are colloidal in nature. The course and rate of enzyme action may be followed by adding invertase to a solution of cane sugar and examining a sample of the liquid from time to time with the polarimeter (p. 94). By these means it is found that when the reaction takes place in a test-tube the rate of change, though great at first, gradually slows down, until finally it becomes so slow that some sucrose is still left after the reaction has gone on even for a great length of time. This is the more surprising in that the enzyme itself has not been destroyed but is still present.

A similar slowing down is exhibited by other enzyme action—as, for example, that of the hydrolysis of starch by diastase. If, however, equal amounts of diastase in solution are added to equal amounts of starch solution, one lot in a glass tube and the other in a parchment tube dipping into a large volume of water, the end-results as measured by the quantities of starch left unhydrolysed are very different in the two cases. In the glass tube hydrolysis may cease while starch still remains, but in the parchment tube it

goes on until all the starch is hydrolysed. Yet the only difference between the experiments lies in the fact that whereas sugar diffuses through the parchment, it remains in the glass tube. The difference, however, is sufficient to account for the facts. The reaction between starch, water, and diastase is a balanced reaction—that is, one which may go on one way or the other according to circumstance. As increased weight at one end of a see-saw prevents the other from coming down, so piling up sugar on the one side checks the action of the enzyme on the other side.



When, however, the sugar is removed by diffusion it ceases to affect the balance adversely, and the enzyme continues to hydrolyse starch.



Or, to put it another way, the colloidal particles of enzyme adsorb starch-water particles, and the hydrolysis is effected catalytically at the surface of the particles; but the enzyme adsorbs sugar also, and in so doing leaves less room for the starch-water particles. The more sugar is produced the more is adsorbed, until finally, though still capable of hydrolysis, the load of adsorbed sugar borne by the enzyme particles prevents the work from going on. The parchment tube, on the other hand, admits of the diffusing away of the sugar. There is less, therefore, for the enzyme particles to adsorb,

and they are in consequence the more free to keep going their business of hydrolysing starch.

Other conditions besides the accumulation of end-products may tip the beam of the reaction the other way: temperature, for example. At normal temperatures the balance of the reaction

$$\text{starch} \rightleftharpoons \text{sugar}$$

effected by the enzymes of the leucoplasts of a resting potato tuber is in favour of starch formation; but when the temperature falls nearly to zero the balance alters and comes to favour sugar production—hence the sweetness of frosted potatoes (p. 93).

It is not easy to account for the potency of enzymes in speeding up chemical change, but there are grounds for believing that the minuteness of the colloidal particles of enzymes in solution is an essential factor in their catalytic action. For there is a wonderful potency in minute masses, and forces are liberated at the surface of things which are not operative in their mass. A wide glass tube dipped into water does not suck it up to any appreciable extent, but if the tube be narrow water rises in it above its level in the outer vessel, and its surface forms a concavity, the edges of which, where they touch the glass, are higher than the rest of the surface film. The surface forms a film or skin which sticks to the glass and hauls up the cohering water underneath. The force thus manifest is spoken of as surface tension. The narrower the tube the higher the water rises in it, that is, the greater is the pull exerted by surface tension. Hence it follows that where the surfaces of things are in contact, forces may be developed, and it may also be inferred that matter when it exists in a very subdivided state—as, for example, as a colloid the sum of the surfaces of the particles of which is very large—will be the seat of very powerful forces. Thus perhaps may be explained the imbibition of water by colloids, and the remarkable catalytic action of enzymes.

The number of enzymes which has been extracted from plants and animals is very great. One group of them hydrolyses starches. They are the diastases or amylases. Another group—the cytases—hydrolyses celluloses; another hydrolyses different sugars, for example, invertase (sucrase) hydrolyses sucrose, and maltase hydrolyses malt sugar. The lipases formed during germination of fatty seeds hydrolyse fats, and another even more important group (the proteolytic enzymes) hydrolyses proteins. Of the proteolytic enzymes some have more clastic action than others, breaking proteins down completely into amino-acids. Proteolytic enzymes and those of the other categories are the common property of plants and animals. Wherever change of food-material is going on there are to be found these specialist speeders-up, each of a special kind of change.

So much for the physical and chemical properties of the food-materials and the manner of the change whereby reserve foods are mobilized and immobilized again by enzymes; it now remains to survey the 'ground' over which the traffic in food-materials passes.

So far as the simple plants are concerned nothing more need be said. In the simplest of all, the unicellular plant, the food-materials made in the neighbourhood of the chloroplast have not far to go, and diffusion, movements of cytoplasm, and adsorption may suffice for their distribution within the cell body. The same agents may be invoked to explain the distribution of food-materials between the cells of a simple multicellular plant, parts only of which are capable of photosynthesis. But as the plant body grows large, and its assimilatory surface becomes more localized, the problem of rapid transport becomes acute.

Diffusion, as has been shown, is a slow process, and it is hard to believe that it suffices to supply sufficient material quickly enough to distant parts of large plants. The problem confronted the massive benthic plants which developed in the sea; it confronts the great seaweeds of to-day, some

of which are of greater length than any other kind of plant; and it confronts yet more acutely all massive land vegetation. Even in the seaweeds the structure and distribution of tissues in those which reach large dimensions indicate that provision has been made for the transport of food-materials. Stretching from the frond-like assimilatory region through the stalk to the attachment organ which fixes the seaweed to the rock are specialized tracts of elongated cells, along which it is reasonable to suppose that food-materials may travel faster than along the shorter cells which make up the rest of the body. For, in the first place, there are fewer cell-membranes to pass; and in the second, streaming movement of cytoplasm, if any were of regular occurrence, would serve to carry food-materials on their way. Whether or no active streaming movement habitually takes place in these cells is not known; but it is known that the cytoplasm of the cells of a plant-tissue may upon occasion become quickened into active movement. As may be seen by watching a living cell under the microscope the more fluid part of the cytoplasm, bearing with it numerous granules, circulates or rotates along the less fluid part of the cytoplasmic mass. Although it cannot be affirmed that cytoplasmic movements play a regular part in effecting the distribution of food-supplies, it is not improbable that they help the food-materials on their way from cell to cell.

However that may be, the evolution of land plants has been attended by the development of well-defined vascular strands along which water and food-materials travel from one part of the plant to another. In mosses which are lowly in stature and in place among land plants, any vascular strands which are formed do not reach a high level of development; but among the ferns, conifers, and ordinary flowering plants, in all of which groups abound plants with the large habit of trees, the vascular strands are conspicuous and of elaborate and varied forms of construction. To describe them all is not necessary, since the vascular system of the flowering

plant illustrates sufficiently well the manner in which the vascular strands serve for the long-distance transport of water and food-materials.

In many kinds of plant, including flowering plants, the

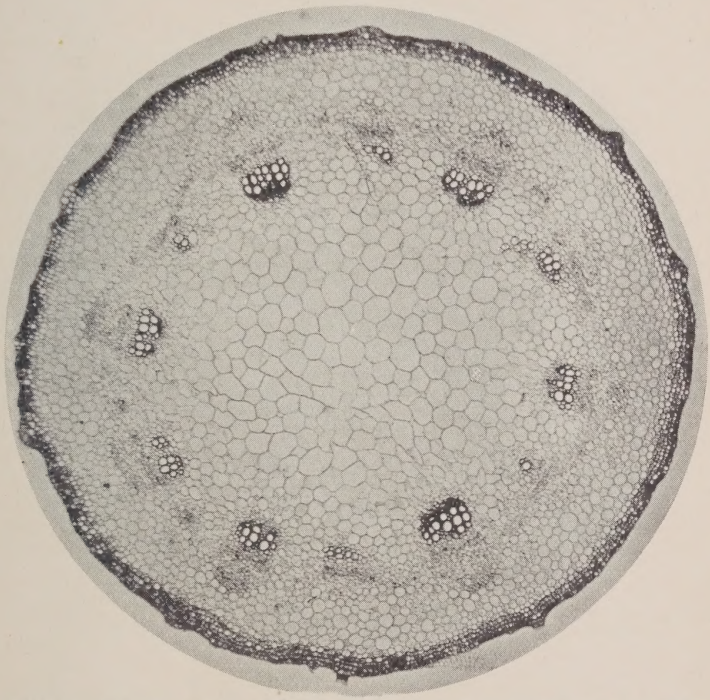


Fig. 23. Transverse section of the young stem of a Dicotyledon, the sunflower (*Helianthus annuus*).

vascular system of the root differs from that of the stem, and among flowering plants the vascular strands of Monocotyledons—palms, grasses, lilies, &c.—present striking points of difference from those of Dicotyledons. Cross-sections of the stem of a seedling dicotylous plant (Fig. 23) show three zones of tissue, each of which may be traced to a layer of cells at the growing-point. The surface zone consists

of a single layer of cells, the epidermis. Below it is the cortex, made up of cells which have undergone in the course of their development no great change in size or shape. Within the cortex lies the central cylinder, composed in part

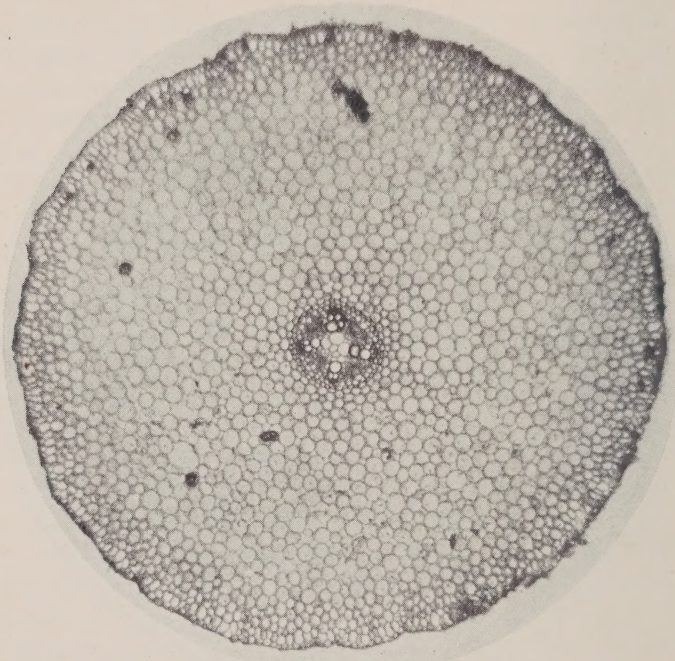


FIG. 24 A. Transverse section of the young root of a Dicotyledon, the buttercup (*Ranunculus repens*), showing superficial layer, cortex, and central cylinder.

of purely cellular elements, and in part of vascular strands. The latter lie in a broken ring, each isolated from its neighbour by masses of cells which, from their ray-like form, and from the fact that they extend to and join with the cells of the pith (medulla), have received the picturesque name of medullary rays. The vascular strands are definite in number,

and may be traced through the stem to the root, where, although differently disposed, they have the same essential structure (Figs. 24 A and B) as in the stem. They extend into

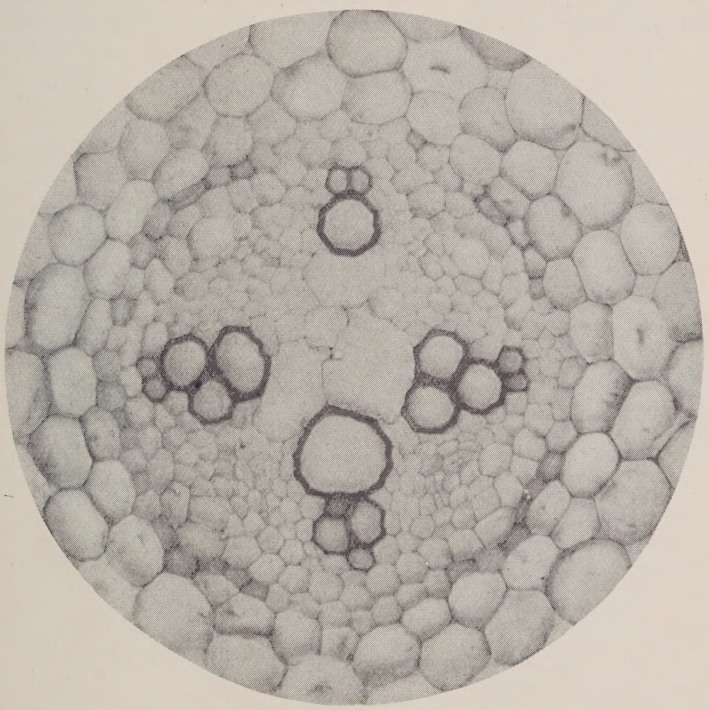


FIG. 24 B. Part of Fig. 24 A more highly magnified, showing central cylinder surrounded by several layers of the large-celled cortex (outer cortex and superficial layer of root not shown). The xylem strands, four in number, alternate each with a phloem strand.

the lateral roots and into the branches and leaves, and thereby bring all parts of the plant into communication with one another.

If instead of a young stem an old one, e. g. a branch of a large dicotylous tree, be cut across, a very different state of

affairs is disclosed (Figs. 29 and 30). Cork, formed in sheets or bands in the cortex, has cut off the epidermal and cortical tissues external to it. Deprived of water and food these tissues, dried and shrunken, constitute the dead bark, which is the more furrowed and massive the deeper down in the cortex the cork

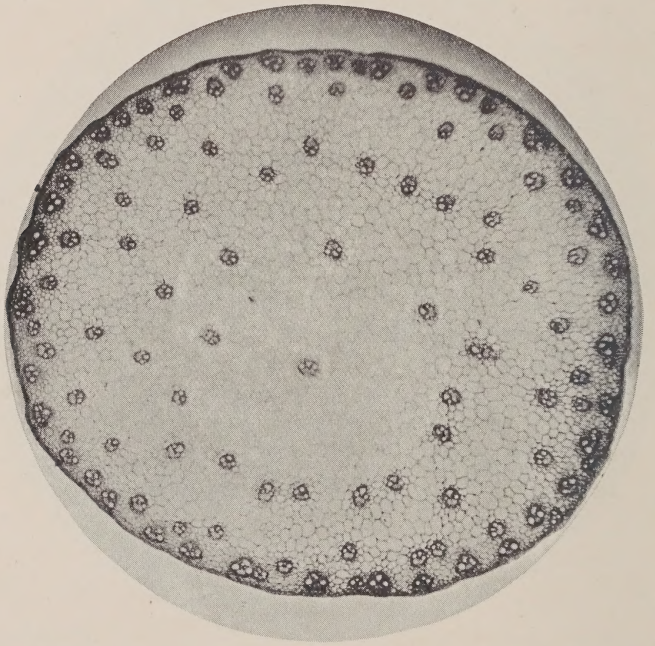


Fig. 25 A. Transverse section of the stem of a Monocotyledon, maize (*Zea mais*), showing the numerous scattered bundles. Cf. Fig. 23.

was formed. Within the bark is the thin residue of cortex, and within that, making up the main bulk of the stem, is the central cylinder, extending almost or quite to the centre, and consisting of a great mass of wood surrounded by a thin mantle of non-woody tissue, which, with the wood, constitutes the vascular tissues.

The structure of a monocotylous stem is illustrated in

Figs. 25 A and B. In the seedling stage the vascular bundles lie, not in a ring, but more or less scattered in cellular ground-tissue (Fig. 25 A), and in an old stem the bundles, although more numerous, remain isolated and scattered. In it in-

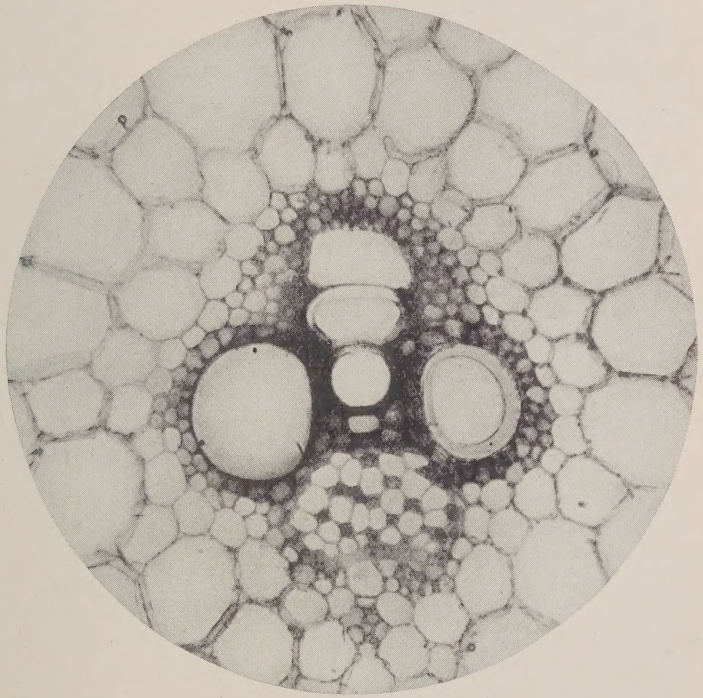


FIG. 25 B. Transverse section of one of the vascular bundles shown in Fig. 25 A. The bundle consists of xylem and phloem with no cambium. Cf. Fig. 28.

creased girth is due to the growth of the cellular ground-tissue in which the bundles lie. Thus it may be seen that whereas in a dicotylous stem the original or primary vascular bundles undergo further development, in a monocotylous stem—even in such massive stems as those

of palms—they, with rare exceptions, do not. All that happens is that as the crown of leaves of a palm or other monocotylous tree increases, more bundles are to be seen in cross-section of the stem; for each leaf may have a hundred or more, and the bundles of the leaves run downwards in the stem, where they join with the original vascular bundles of previously formed leaves.

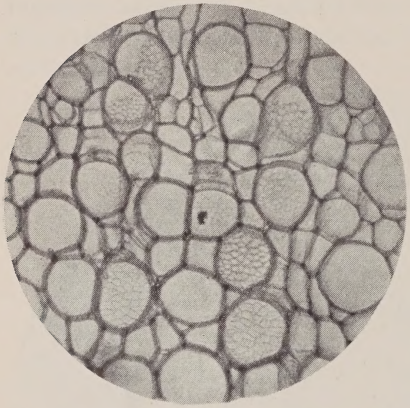


FIG. 26. Transverse section of phloem of *Cucurbita Pepo*, showing sieve-plates.

FIG. 27. The sieve-tubes of *Cucurbita Pepo* in longitudinal section.

The mode of increase of the dicotylous vascular bundle may be observed by examining stems in successive stages of development. At the tip of the stem lies the growing-point, a mass of embryonic tissue consisting of unmodified cells. A little way behind it the vascular strands begin as tracts of elongated cells, lying in a broken ring and surrounded by the cortex. They are known as procambial strands. Farther back the vascular bundles are developing. Those cells of a procambial strand which face towards the centre of the stem undergo change and give rise to woody elements. The first-formed

woody elements are known as the protoxylem Farther back still, other cells of a procambial strand have likewise developed into woody elements, and so on until a mass of wood—the primary xylem—is formed. Meanwhile changes have also occurred in the cells on the outer side of each pro-

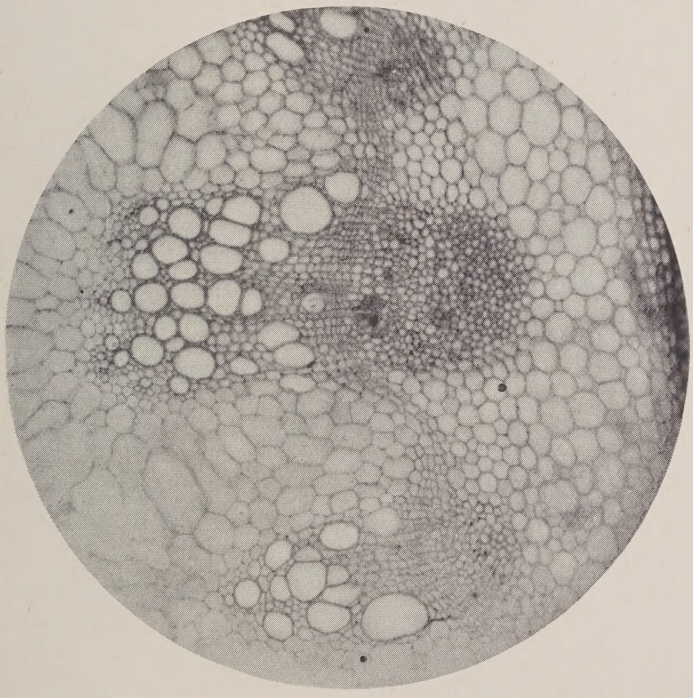


Fig. 28. Transverse section of part of the stem of *Helianthus annuus*, showing vascular bundles with continuous cambium ring (cf. Fig. 23).

cambial strand. Some of them have given rise to remarkable tubular elements which are known as sieve-tubes (Figs. 26 and 27).

In this manner is formed each of the bundles shown in Fig. 23.

During the first year the cells of each procambial strand of the stem of a dicotylous plant continue activity until they have produced a vascular bundle, consisting of three essential parts: a sieve-tube tissue known as primary bast or phloem, outermost; a woody tissue, the primary wood or xylem, innermost; and lying between them layers of cells of the procambial strands which have retained powers of growth and division. These last constitute the cambium (Figs. 23 and 28). In a monocotylous stem, on the other hand, all the cells of each procambial strand are involved in the production of wood and bast (Fig. 25 B). When the primary bundle is complete no cambium is left, and hence the vascular bundle grows no more.

It is very different with dicotylous stems. In them the cells of the cambium lying between the bast and wood retain powers of growth and division, and form several layers. Of these layers those lying nearest the primary xylem give rise to wood elements (secondary wood), and those lying nearest to the primary phloem form secondary bast. Thus by intercalation of new elements both wood and bast are increased. The increase is augmented by another means also. In some unknown way, as a result of the activities of the cambium within the vascular bundles, the cells of the central cylinder in touch with it reassume power of division. They grow and divide, and give rise to layers of cambium-like cells, so that cambium now takes the form of a more or less continuous ring (Fig. 23). As the cambium layers of the bundles give rise to wood and bast so do those between the bundles. The wood and bast produced within the bundles are continuous each with the corresponding wood and bast produced by the cambium between the bundles, and hence the vascular system comes to consist of a more or less continuous, hollow cylinder of wood within, bast without, broken only by narrow rays—the remains of the primary medullary rays (Figs. 29 and 30). Year in, year out, as spring returns the cells of the cambium-layer resume activity, divide and

produce new wood-forming layers on the inner and new bast-forming layers on the outer side. So active is the cambium, and so great are the powers of division of cambial cells, that a branch of almost any woody shrub or tree removed at the proper season may be grafted on the stem of another plant of the same or even of a different species ; provided only that the two cambiums make contact with one another. And so also is it that the wound made by the lopping of a branch of a tree heals itself in course of time by the formation of wound-tissue chiefly by the cambium ; spreading each year more and more over the exposed surface the wound-tissue comes eventually to cover the wound.

Each year when the bark is withered and dead it may remain on the tree, stretched and riven with fissures, or it may be cast off. In either case the pressure set up by the growth of the wood and bast in the previous year is relieved, and hence when the cambium renews its activity in spring, space for development is there. At this time, however, food-materials are required everywhere by the bourgeoning tree, and so cannot be spared freely to the cambium. There is need, too, for a rapid conduction of water to the young unfolding buds, and thus it is that spring wood has large cavities and thin walls. Its prime business is to conduct plenty of water. As the year's growth goes on, the new wood and bast, which together imprison the cambium ring, exert increasing pressure on it. Working against pressure, albeit with plenty of food-material, the cambium now makes wood-vessels with narrow cavities and thick walls (Fig. 30). They are *par excellence* skeletal in function, giving support to the increasing fabric of the tree. Hence it is that in a climate with alternating seasonal change of winter and summer the age of a tree may be known by the number of its annual rings. The thick-walled, narrow vessels of autumn make such a contrast with the thin-walled, wide vessels of spring that the line of demarcation is visible to the unaided eye. Nay, more, it is claimed, perhaps justly, that the annual vicissitudes of

the climate of ten and more centuries are to be seen reflected in the different dimensions of the successive annual rings of trees like the big tree of California (*Sequoia gigantea*) which live and endure for upwards of one thousand years.

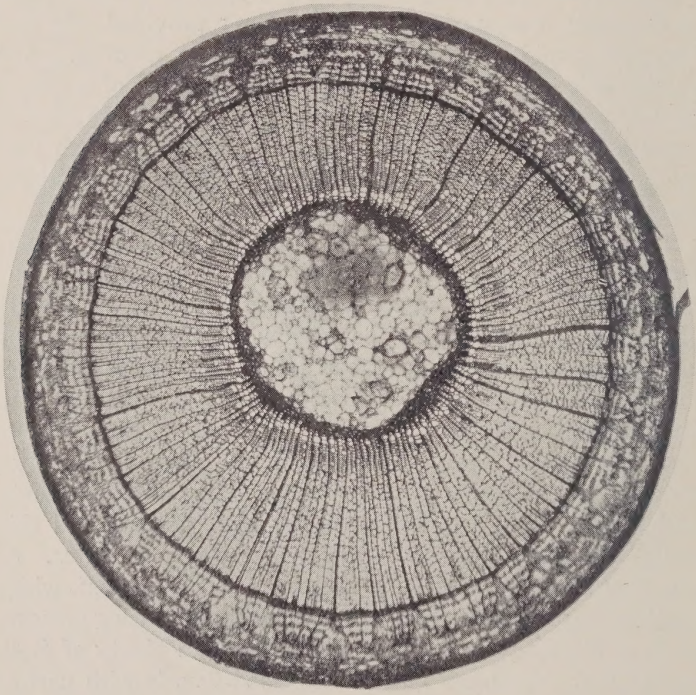


FIG. 29. Transverse section of the stem of the lime (*Tilia europaea*) in its second year, showing continuous woody cylinder extending inwards to pith and outwards to cambium, with medullary rays running radially through it. Outside the cambium, the bast surrounded by remains of cortex and the bark.

So much for the large architectural plan of the conducting tissues: now as to details. The characteristic elements of wood or xylem of flowering plants (Angiosperms) are known as vessels (Fig. 31), but the wood contains cellular elements as well, and may also contain long and strong fibrous

elements—woody fibres—formed each by the growth and change of a single cell. Vessels are long, tubular, woody-walled, dead elements, the cavities of which contain water, air and water, or in the older parts air only. They may, in

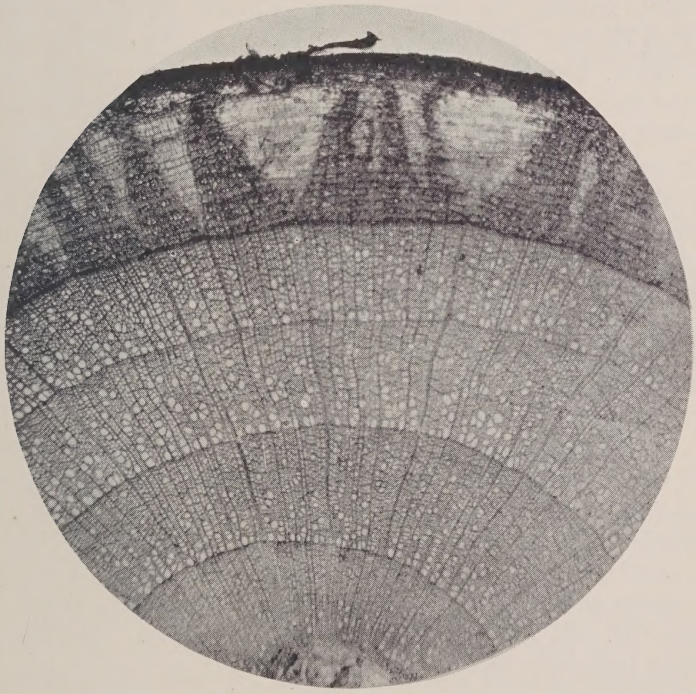


Fig. 30. Transverse section of part of the stem of the lime in its fourth year, showing annual rings (see text).

the case of some trees, attain to a length of several yards, though they are generally much shorter; but in any case vessels are many times longer and wider than the cellular elements from which they are formed. They communicate freely with one another in a longitudinal direction, and thus form a system of aqueducts stretching through the

plant. A vessel is formed by the synchronized development of a longitudinal row of cells derived from cambium cells. Each one of the vessel-forming syndicate grows in all directions, but particularly in length. The cytoplasm forms woody substance, lignin, which, deposited on the walls, imparts to them greater strength whilst leaving them elastic. The deposition of lignin on the walls is not uniform, but takes curious forms. It may be spread all over the wall, except for certain small areas, so that a pitted vessel is formed; or the lignin may be deposited in a spiral, or as rings, to produce spiral or annular vessels. Thus the plant obeys Nature's common law of economy and efficiency. The localized thickenings give support to the wall, the thin places between them allow water to pass into or out of the vessel. With the completion of growth and the plastering of the walls with lignin the life of the cells of the wood-forming syndicate comes to an end. Cytoplasm and nucleus disappear, and their death consecrates the vessel to the mechanical purpose of water storage and conduction.

The sieve-tubes (Figs. 26 and 27, p. 122)—the chief elements of the bast—are also formed by a syndicated longitudinal row of cells, but the mode of their formation differs from that of wood-vessels. Each component cell divides laterally to form a small companion cell, which, though it does not grow much, remains associated with the sieve-tube segment from which it was cut, and retains its nucleus and cytoplasm. This done, each sieve-tube segment, without much change of its longitudinal walls, but growing greatly in length, drills holes, no doubt by the agency of enzymes, in the party wall between itself and the next sieve-tube-forming cell. The cross-walls become perforated, sieve-wise—hence the name—and the cytoplasms of neighbouring components communicate with one another through the sieve-plate (Fig. 26), so that through the system of connected sieve-tubes which runs from end to end of the plant, cytoplasm is continuous. Strange to say, however, in the course of formation of the sieve-tubes the nucleus of each component

cell disappears and the cytoplasm alone remains. It happens in certain dicotylous plants, when they are going into rest in autumn, that the sieve-plates are closed by the deposit on them of a shining white substance—callus. Communication thus interrupted may never be reopened. The life of a sieve-tube is, in any case, short. It dies crushed between the upper and the nether millstone—the bark and the wood. But in some plants when spring comes the callus is dissolved away, and the sieve-tubes become capable of functioning for a second season. Not all the bast-forming cells give rise to sieve-tubes. Some remain cellular, and others may give rise to bast fibres: indeed, it is from the latter that hemp and various other fibres used in industry are obtained.

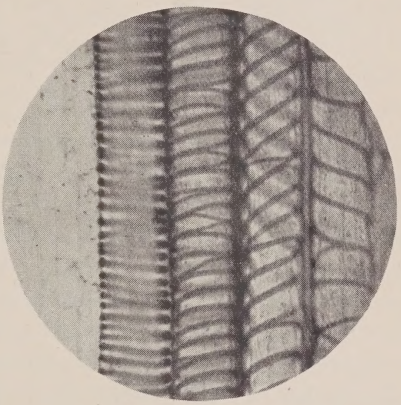


Fig. 31. Longitudinal section of the wood of the sunflower, showing vessels with spiral thickening.

The steadily increasing vascular system plays many parts in the life of the plant. The woody walls of vessels and woody fibres together form an internal skeleton. The living, cellular elements of wood and bast store surplus food-materials. They possess leucoplasts, and hence may ring the changes on carbohydrates from mobile sugar to storage starch, and back again to sugar. The vessels of the wood, and particularly of the young wood, constitute aqueducts for the transport of water, and also reservoirs for its storage. They also serve for long-distance transport of raw and elaborated food-materials. The mineral substances absorbed by the root pass into the vessels, and are transported in solution in the water-current to the leaves; so also—in spring at all

events, when the sap rises—sugars formed from starch stored in the cellular elements of the wood of root and stem are carried to the unfolding leaves. It may be that the wood vessels take part also in the transport of such food-materials as sugar, not only upward from the root to leaves, but downward as well—from the leaves to the stems and underground organs.

The part played by the sieve-tubes in the conduction of food-materials is more obscure. If a branch cut off from a tree be placed in water after a ring of 'bark' down to the wood has been removed from it, water ascends and keeps the upper parts fresh and green, but the food-materials made by the leaves do not descend below the edge of the cut, and hence though the parts above the ring grow, those beneath it do not. By other more elaborate methods of removing one or other of the tissues of stems evidence has been obtained which suggests, albeit not with absolute certainty, that the sieve-tubes play an important part in the distribution of sugars and nitrogenous food-materials. The companion cells of the sieve-tubes may be regarded as sidings for local transhipment of materials. Partly through the water-current in the wood, partly via sieve-tubes, and finally from cell to cell by diffusion, the mobilized food-materials reach all the living cells of the plant. Thus do they arrive at their appointed destination.

VI

The use of the food-materials for construction and power-production. Growth and differentiation of cells and tissues. Respiration. Aerobic and anaerobic life. Fermentation and decay. Self-supporting (Autotrophic) and non-self-supporting (Heterotrophic) flowering plants: Saprophytes, Parasites, Semi-parasites. Symbiosis. Insectivorous plants.

THE food-materials synthesized by the plant are mobilized and brought by the transport system within reach of every living cell. Those materials to which the plasmatic membrane is permeable pass into the cell, and are either used at once or stored to meet subsequent needs there or elsewhere. The uses to which the food-materials assimilated by living cells are put are manifold. The materials may serve for the construction of cytoplasm, nucleus, plastids, cell-walls or other parts of the cell, or, undergoing downgrade chemical changes, they may be resolved into the simpler substances from which they were originally derived, and in the process yield to the plant the energy locked up in them.

The work of construction carried on by vegetation is as great as it is varied. From a microscopic, unicellular embryo a gigantic tree made up of myriads of cells arises. All the mass of its woody and other tissues, as well as the living substance of cytoplasm, nucleus, and plastid, is the product of age-long constructive activity of the protoplasm. In order to grow up, or even to grow at all, the plant must perforce carry on a multitude of physico-chemical operations. Proteins and other food-materials must be incorporated with the protoplasm, thereby augmenting it. Plastids must receive sufficient protein and other material to permit of their almost indefinite multiplication by division, chlorophyll must

be manufactured, walls must be laid down between the dividing cells, and the tenuous cell-walls originally formed must needs be reinforced by the deposition on or in them of additional cell-wall substance—it may be cellulose, lignin, cutin, or suberin.

At any moment circumstances may require the presence of enzymes at this or that spot; here to hydrolyse starch, fats, or proteins, and there to perforate the plates of sieve-tubes. The numerous enzymes which the plant employs are secreted by protoplasm, and, needless to say, at material loss to itself. Repair as well as new construction must therefore continually preoccupy the plant, and all the time internal conditions of temperature as favourable as possible to the performance of chemical work must be maintained. For these conditions to be secured not a little of the energy which the plant liberates by breaking down its laboriously synthesized food-materials must take the form of heat. In its early stages of development the flowering plant may draw upon the food-materials stored in the seed as the result of the manufacturing energy of the mother-plant. The endowment, as has been shown, takes the form of starch or other carbohydrates, or fats, and also of proteins which occur in larger or smaller quantity in seeds. In those seeds which serve mankind as sources of food the reserves are large and conspicuous, as witness the starch and protein grains stored in the cells of the cotyledons of the seeds of legumes (peas, beans, &c.), and the special layer of cells (aleurone grain layer) containing large protein granules in wheat and other cereals (Fig. 8 B, p. 32).

Plants with fatty seeds make yet more elaborate provision of food for their offspring. The seeds of the almond, castor-oil plant, Brazil nut, &c., contain not only fat, but also large aleurone grains, partly composed of proteins and partly of mineral substances—chiefly calcium and magnesium phosphate. The proteins may occur in two states—as a granular matrix and a crystalloid, that is, a large, clear, crystal-like mass lying in the matrix (Fig. 32).

But even in the most richly-endowed plant the food-reserves are soon exhausted, and thenceforth the seedling must fend for itself. Other less fortunate seed-plants are born poor in reserve food-material, and have to make their own living almost from the start. In this respect they are much on a par with plants of lower groups which, not having evolved the habit of seed-formation, begin life with little or no endowment of food-material.

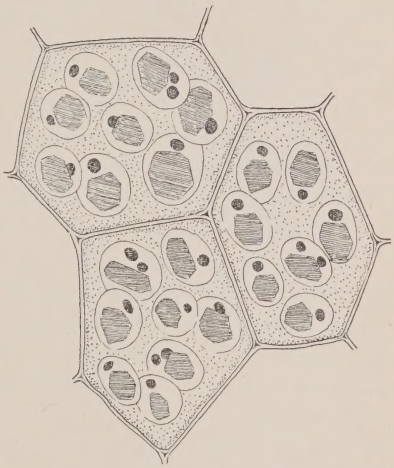


Fig. 32. Cells of the endosperm of the castor-oil plant (*Ricinus communis*) with aleurone grains embedded in cytoplasm. Each grain consists of a crystalloid (lightly shaded), and globoid (heavily shaded) lying in a protein matrix (unshaded).

Evidence of the varied constructional work carried on by protoplasm is furnished by the amount and diversity of the by- and waste-products — many containing nitrogen —which are formed and deposited in the plant as a result of its chemical activities. The accumulation of these numerous substances is to be accounted for by the fact that plants, unlike the generality of animals, possess no well-defined excretory system serving for the riddance from the body of waste products. But, inasmuch as the living body of a perennial plant contains tissues which have ceased to live, waste-material is not infrequently dumped and accumulated therein —chiefly in old heart-wood and in bark. Some waste products—for example, alkaloids such as thëine, caffëine, nicotine, quinine, and those of opium—though their use to the plant is obscure, are of great value to mankind as stimulants,

drugs, and poisons. Others almost certainly serve useful purposes in the plant. Poisonous alkaloids deposited in the bark or wood may act as natural antiseptics, preserving trees from decay or protecting them from attack by boring and other insects. Among by-products of protoplasmic activity which may also serve similar purposes are the numerous class of cyanophoric glucosides: substances which, when hydrolysed, yield sugar and the highly poisonous gas hydrogen cyanide (HCN). They are of wide occurrence—in bitter almonds, the leaves of laurel, and many other plants. Accompanying the glucosides, but in intact tissues separated from them, are glucosidal enzymes, each of which splits the glucoside with which it is associated into sugar, hydrogen cyanide, and other substances. It may be assumed therefore that, whereas in the uninjured tissues, since the enzyme cannot 'get at' it, the glucoside remains unchanged, in tissues injured by parasites enzyme and glucoside are brought into contact with one another and the latter is hydrolysed; so that there is sugar to lure the pest and poison gas (hydrogen cyanide) to destroy it.

Of the manner of growth of protoplasm—or, for that matter, of any other living part of a cell, or even of its non-living cellulosic wall—little can at present be said. They, like Topsy, just grow. It is convenient, however, to emphasize the difference between growth and differentiation. The one connotes increase of cytoplasmic, nuclear, and plastid living material; the other, the (usually irreversible) change of size and form of cells and tissues which takes place during the development of the plant. Differentiation may be accompanied either by an increase or decrease of the mass of living material.

Illustrations of growth and differentiation are provided by any young and active member—root, stem, or leaf. In the root, for example, the growing-point, covered by the root-cap (Fig. 33), consists of a mass of similar cells rich in cytoplasm, each with a large nucleus and a delicate cell-wall. The cells of the embryonic or merismatic tissue of a growing-point undergo division each into two cells. Certain of the

daughter-cells remain embryonic. They grow, and when protoplasm and nucleus have increased sufficiently each embryonic cell divides again, and so on, it may be, dividing and redividing during a thousand years or more. So long as the

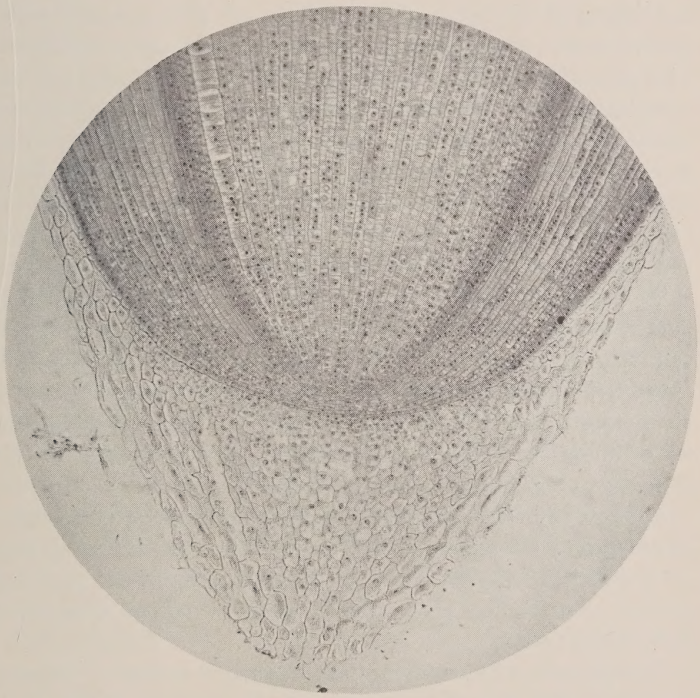


Fig. 33. Longitudinal section through root-tip of maize (*Zea mais*), showing merismatic tissue of growing-point covered by the root cap.

plant endures the embryonic cells of the growing-points divide and grow and divide again. Those daughter-cells which do not remain a permanent part of the growing-point behave differently. They increase beyond the size of embryonic cells. The increase is indeed so great that it outpaces that of the cytoplasm, which in consequence no longer fills

the cell-cavity (Fig. 21, p. 103). The osmotic substances in the cell-sap absorb water. The cell-wall is stretched. In the interstices and on the surface of the colloidal cell-wall, cellulose, secreted by the cytoplasm, is deposited, and as a consequence the cell-wall increases in all dimensions. The stretching of the cell-wall by the osmotic absorption of water is reversible. If a growing root be put in an osmotic solution of a strength a little greater than that of its cell-sap, water is withdrawn from the cells and the root shortens. In this contracted condition the root ceases to grow; but if it be transferred to water the cells elongate once again and growth is resumed. If the root be placed again in the osmotic solution the cells of the elongating region do not shorten so much as they did before. Part of the stretching or extension of the cell-walls brought about by osmotic pressure has in the meantime been made permanent: yet the cell-wall may still be stretched osmotically, and of this further extension part may again be made irreversibly permanent. So that by the dual process, stretching by osmotic pressure and infiltration and plastering of cellulose secreted by cytoplasm, the cell-walls of the elongating region may attain to large dimensions.

Beyond the region of elongation in the root lies the region of secondary change, in which groups of cells, now demarked as a series of tissues, undergo differentiation into root-hair cells, cortical cells, procambium cells, wood or bast cells, sieve-tubes, vessels, and so on.

The process of elongation just described serves to account for the astonishing rapidity with which plants may increase in length. Bamboos, for example, in tropical countries may be *seen* to grow. Within a few days after the advent of the rainy season the massive buds destined to form new canes begin to unfold, and shoot up as great grass-like stems which in the course of the growing season reach a height of a hundred feet or more. A pin stuck in the large growing bud and watched for a few seconds through a fixed tube with a plain glass end may be seen to be moving upwards. The move-

ment is the resultant of the elongation of a series of cell-layers at each of the many nodes of the immature shoot of the bud. Each cell of these layers elongates, and the sum of the simultaneous, albeit minute, elongations of the many cells of the numerous layers is sufficiently large to make growth visible.

In this account of the constructional activity of protoplasm it will be apparent that much ignorance underlies a thin veneer of knowledge. Little is as yet known of the physico-chemical constitution of the constituents of living protoplasm, and although the study of the properties of colloids is beginning to throw light on the dark places of the cell's protoplasm, the light is as yet uncertain and dim. The nature of life still escapes understanding, and judgement whether a thing is alive or dead is based only on observation of its behaviour. If able to build, repair, and multiply its body by using materials which, though of definite kinds, lack separately, or, even when mixed together, the essential properties of a living substance, it is inferred that the thing is alive. A crystal may grow if immersed in a solution of the substance of which it is composed; but the growth of a cell is a more complex affair, involving the picking out from its surroundings, assembling and piecing together of numerous substances which, although they contain the essential elements, are acquired in simple form and undergo elaborate synthesis in the plant.

The behaviour of the living organism possesses also the distinctive feature of appositeness; it is not mechanical and unchanging, but has reference to the well-being of the organism. The tip of a pine stem grows vertically upward, and the lateral branches stand out horizontally. But if the leader be removed, a lateral branch may rise up and take its place (see p. 227). It is customary and convenient to liken living organisms to mechanism, and in view of the marvellous developments of mechanism it would be rash to dispute the justice of the comparison; but at the same time it must be confessed that the complexity of behaviour of any living organism

is far greater than that of the most elaborate mechanism contrived or imagined by man. If army tanks could be made which, without a crew to work them, would advance and retreat in obedience to the dictates of good tactics, live on the country more absolutely than Napoleon's armies: if they could fire and replenish their guns from synthetically produced ammunition, right themselves when overturned, and repair the damage: if they could pair and beget corps of tanks, each growing from microscopic beginnings into mature form like that of the begetters: and if they could in fullness of time evolve both higher, more complex types, and also lower, simpler ones which yet would prove effective in some fields of action—then the tank might serve as a rough working-model of a living organism.

No less than for power of self-construction, the living organism is remarkable for its powers of self-suppression and self-destruction. At each phase of development of a plant, tracts of tissue become differentiated, all or many of the cells of which forgo the power of continuous cell-division which resides in the embryonic cells from which they were formed. In some instances the power is only in abeyance, and may in certain circumstances be resumed. For example, a single cell of a leaf of a begonia may become embryonic, undergo division, and give rise to a new plant. In other instances, however, the embryonic power of cell-division is altogether lost: as it is, for example, by the wood-forming cells, which can only qualify themselves to take part in the conducting of water by the lignification of their walls and the death of their cytoplasm. Thus, in the cells of plants, as among mankind, specialization spells limitation, and limitation of general powers owing to intensive exercise in a special direction may mean either suppression or loss of those general powers. They may be lost for good and all, or, as with the cells of the cortex which give rise to cambium cells (p. 124), a stimulus may suffice to call forth the general powers of growth and division unimpaired after their long suppression.

What holds good for cells and tissues may also be true of the whole plant. An annual plant, having set seed, dies. No one knows why. If prevented from setting seed—as, for example, by disbudding the flowers as fast as they form, or by interfering with flower-formation by excessive watering—the annual may live for several years. Herbaceous perennials die down each year after flowering; but what brings about the death of each year's shoots is unknown. The interests of the plant require it and the sacrifice is made, for manifestly it is a convenient way of wintering, to retreat below ground safe from drying winds and hard weather with all life dormant.

Every leaf which flutters to the ground in autumn carries with it a mystery. It is well for the plant that the leaves should fall before winter comes and so reduce risk of desiccation. The plant makes sure that the leaf shall be evicted. It cuts off the water-supply by forming a layer of cork near the base of the leaf stalk—an absciss layer. But how vegetation first passed such severe sumptuary laws can at present be but a matter of speculation. The law of leaf-fall holds only in countries of alternating wet and dry, or warm and cold climates. Where climate is uniform the writ does not run. There, leaves, as a rule, remain evergreen and attached to the tree till, after some years, one by one they fall from old age.

The power of orderly self-destruction exhibited by plants reaches extreme expression in cells or tissues or whole plants subjected to starvation. Cut off from supplies of food, a cell continues for a time to live. Gradually all its reserves of food are used up, and yet it lives; feeding, literally, upon itself. In these circumstances energy and material are derived from the breaking down of cytoplasmic and nuclear material, and not until the breaking down has gone far is recovery impossible and death inevitable.

In normal conditions, however, the plant obtains needful energy by less drastic methods. In the sugar molecules formed photosynthetically are locked up the stores of energy made latent during the synthetic process. To release these

stores is the constant work of the active cells of plants and animals. The process, which is called Respiration, occurs in one form or another in all actively living organisms. For life may manifest itself only if the living organism have energy at its disposal.

In the green plant the main source of supply of energy lies in the carbohydrate (or sometimes the fatty) food-materials. Respiratory decomposition of carbohydrates, and consequent release of energy, may be demonstrated in germinating seeds, or in any parts of plants, leaves, expanding buds, flowers, &c., in which life is active. To show it, care must be taken to prevent the process of respiration from being obscured by that of photosynthesis, and this may be done either by choosing for the experiment non-green parts of plants or by excluding light from such as are green. Seeds begin to respire so soon as enough water has been absorbed to quicken them into activity. By the use of the baryta-water apparatus described on p. 60, it may be demonstrated that carbon dioxide is given off continuously and in large quantities from the germinating seeds. With the evolution of the gas there is a steady diminution of storage carbohydrate. The longer the plants are kept in darkness, the more the stores of carbohydrate are depleted, and, in consequence, the more the dry weight decreases. The continuous evolution of carbon dioxide is dependent on a supply of oxygen. If the germinating seeds be denied access to oxygen, growth and evolution of carbon dioxide are interrupted. That a close relation exists between oxygen absorbed and carbon dioxide evolved is to be inferred also from the fact that in starchy seeds the volume of carbon dioxide given out is approximately equal to that of oxygen absorbed: molecule for molecule—for one of oxygen acquired, one of carbon dioxide is evolved. It is as though respiration might be represented by the equation:

$$\underset{\text{sugar}}{C_6H_{12}O_6} + 6\,O_2 = \underset{\substack{\text{carbon}\\\text{dioxide}}}{6\,CO_2} + \underset{\text{water}}{6\,H_2O}$$

If respiration is indeed—as the equation suggests—comparable with combustion it should be possible to demonstrate that respiration is accompanied by evolution of heat. This may easily be done. To demonstrate heat-production during respiration it suffices to fill a thermos flask with sterilized seeds previously made plump by soaking in water. A thermometer dipping into the flask and held in place by cotton-wool registers, as germination proceeds, a rise of several degrees. Other parts of plants—leaves, for example—show a similar rise of temperature. A mass of leaves packed tightly together in a felt-covered box gives rise in these abnormal conditions to so great an increase of temperature that the leaves may be killed. Unsterilized seeds may show in a thermos flask an even greater rise of temperature than that exhibited by sterilized seeds; for mould-fungi and bacteria also respire, and in so doing evolve heat. They find congenial conditions for growth on and in the closely packed seeds, increase and multiply there, and betray their presence by the heat of respiration to which they give rise.

By putting all these facts together the nature and significance of the respiratory process become manifest. The living cells of the plant absorb oxygen and bring about a combustion of sugar with the formation of carbon dioxide and water and a release of energy.

Although the equation just given may serve to represent the beginning and the end, it tells nothing of the intermediate stages of the reaction. To kindle starch or sugar into burning requires heat, and it is certain that enough heat to set them on fire is not available in the living cells. But knowledge of the part played by catalysts in the chemical processes of plants suggests that the respiratory destruction of sugar at ordinary temperatures is due to the agency of enzymes. The conjecture finds support in the fact that oxidases—that is, catalysts which promote oxidation—occur commonly in plants. The browning of a peeled apple and of withering leaves, and the blackening of potatoes during boiling, are

examples of the action of oxidases on certain of the contents of these plants which, when they unite with oxygen, happen to give rise to dark pigments. It would therefore seem probable that the plant contains agents—respiratory enzymes—which speed up the oxidation of sugar or other respiratory material. Nor is evidence lacking that the respiration of carbohydrates is effected by special catalytic agents, for it is possible so to treat a plant that, although its protoplasm is destroyed, carbon dioxide continues for a time to be evolved. The evolution goes on fastest when oxygen is supplied, but it may occur also, albeit at a slower rate and for a shorter spell, even when no oxygen reaches the plant.

Here is a new fact: the respiratory evolution of carbon dioxide without oxygen! It, moreover, does not stand alone. Since Pasteur's famous discoveries concerning yeast, it is known that plants (anaerobes) exist which may live in the absence of oxygen. It is known also that the living tissues of higher plants may evolve carbon dioxide even when kept in an atmosphere free from oxygen. When this happens evolution of carbon dioxide is accompanied by the appearance in the tissues of alcohol (C_2H_5OH) in sufficient quantities to be recognizable by its characteristic smell and chemical reactions. The change may be represented by the equation:

$$\underset{\text{sugar}}{C_6H_{12}O_6} = \underset{\text{ethyl alcohol}}{2\,C_2H_5OH} + \underset{\text{carbon dioxide}}{2\,CO_2}$$

It is a clastic or molecularly disruptive change. The sugar molecule is broken down, but in the absence of oxygen the disruption is not complete, and therefore, instead of all the stored energy being released, as is the case with the complete respiratory combustion of sugar to water and carbon dioxide, only part of the energy is set free. The remainder is stored in the alcohol molecule: a fact made patent when, by burning, alcohol, uniting with oxygen, gives rise to water and carbon dioxide and liberates energy.

Respiration without oxygen is therefore an expensive

process. To supply a given amount of energy, more sugar molecules must be disrupted than when oxygen is available and the combustion of sugar is complete.

The formation of alcohol by the tissues of ordinary plants in the course of respiration without oxygen suggests that there is some relation between anaerobic respiration in general and the process of fermentation as carried on by yeast; for in that process also sugar disappears and alcohol and carbon dioxide are produced. The yeast plant (see p. 24) is indeed far more adept than are most plants in the art of living without oxygen. When supplied with oxygen and appropriate food-materials yeast thrives well enough. Its cells grow, undergo division, and give rise to great masses of yeast. In these circumstances, however, the individual yeast-cells produce but little alcohol. The sugar they consume is for the most part oxidized completely to carbon dioxide and water. But when yeast is transferred to a medium containing similar food-materials but no oxygen it behaves very differently. The rates of growth and cell-division fall off, but the production of alcohol by each cell becomes much more rapid. Life without oxygen is no easy matter even for an anaerobe. The yeast-cell continues to live, but can only obtain energy by the relatively extravagant process of breaking sugar molecules into alcohol and carbon dioxide. Incidentally, however, the excessive production of alcohol has its advantages to the yeast plant. Yeast can stand large quantities, whereas most other organisms capable of living without oxygen cannot, and so by brewing strong liquor yeast holds its own against all, or at least most, competitors. The agent whereby the yeast-cell breaks down sugar with the ultimate production of carbon dioxide and water may be extracted from it and used to do similar work. When yeast-cells, pounded in a mortar till the cell-walls burst and the contents escape, are subjected to high pressures, the expressed yeast juice, although it contains no intact yeast-cells, sets up active fermentation of sugar, splitting it, as does the living yeast-cell, into alcohol

and carbon dioxide. The enzyme-like, catalytic agent known as zymase which brings about the fermentation may also be obtained from yeast by chemical methods involving the complete destruction of the cell protoplasm, and so readily that preparations known as zymin which contain zymase are now in commercial use.

Study of the details of the alcoholic fermentation of sugar by yeasts and other micro-organisms—for yeasts are not alone in the possession of this power—has led to great advance in the knowledge of the physiological life-histories and peculiarities of the micro-organisms which set up fermentation, and has also thrown new light on the chemistry of respiration. Thus, it has been found that different species of yeasts have different powers of fermentation. One species ferments dextrose but not cane sugar (sucrose), other, which contain invertase, bring about the fermentation of cane sugar as well as dextrose, other again have powers of wider range and ferment maltose also. Hence it is possible to use yeasts or other micro-organisms possessed of restricted powers of fermentation to sort out one sugar from another. Ground in the mill of the yeast plant, one may be taken and the other left. The classical example of the selective power of micro-organisms is that discovered by Pasteur. A species of the mould-fungus *Penicillium* may be cultivated on racemic acid, which inasmuch as it consists of dextro- and laevo-tartaric acids is optically inactive. With the growth of the *Penicillium* the medium becomes laevo-rotatory owing to the fungus taking the dextro- and leaving the laevo-tartaric acid.

From the knowledge already gained of the chemistry of fermentation it is clear that the process is a complex one, taking place in several stages, and involving the production of numerous intermediate substances. It is therefore probable that normal respiration as carried on by the green plant or by animals is also complex and serial. It can scarcely be doubted, moreover, that anaerobic respiration set up by the cells of green plants deprived of oxygen is initiated by an enzyme-like

catalyst of powers similar to those of zymase, and it is at all events very probable that this process also occurs in normal respiration. On this view the respiration of a plant or animal cell takes place in stages. In the first phase, sugar is transformed into alcohol and carbon dioxide : a change which does not involve the presence of oxygen. In the second phase occurs the oxidation of alcohol (or of some substance which if unoxidized gives rise to alcohol) with the production of carbon dioxide and water.

1. $C_6H_{12}O_6 = 2\ C_2H_5OH + 2\ CO_2$
   dextrose alcohol carbon dioxide

2. $C_2H_5OH + 3\ O_2 = 2\ CO_2 + 3\ H_2O$

In normal respiration sugar is not the only material which may be consumed. Many seeds contain reserves of fats in place of carbohydrate. When germination begins, fat-splitting enzymes make their appearance in the seeds and hydrolyse the fats each into glycerine and a fatty acid, which materials are used directly or indirectly both for constructional and energy-releasing purposes. Finally, when all reserves have been exhausted, the starving cell may still obtain energy by breaking down its proteins ; but when the destruction involves the rending of the protoplasmic fabric life comes to an end.

It need scarcely be said that respiration, although specially vigorous in them, is not confined to germinating seeds. It occurs also, albeit often at a slower rate, in all parts of the plant. Indeed, every living cell whatsoever must perforce, if it is to continue to live, carry on its own energy-releasing operations, either by oxidizing sugar or by splitting it, or by attacking some other substance rich in energy, and decomposing it with the production of waste-substances poorer in energy.

The respiratory activity of the green leaf deserves special consideration. When a bud opens and the miniature green leaves unfold, they are rich in food-materials. The chlorophyll apparatus, though developed, takes a little time to get into working order. During that time the reserve food-materials

are used up in constructional and respiratory work. Soon, however, photosynthesis begins, and each day large quantities of carbohydrate are produced in the green cells of the leaf. On these newly acquired supplies, the leaf itself has first claim, and continuously throughout the day and night some carbohydrate is used in respiration and in cell-construction and repair. Even so, however, there is large provision left to meet the needs of the rest of the plant. Though the work of transport of the surplus supplies is carried on unceasingly throughout the day, it is not completed by evening, but continues throughout the night, so that by daylight the green cells are more or less unencumbered by carbohydrate reserves and are free to resume manufacture. During daylight, therefore, the leaf carries on simultaneously the two processes of assimilation and respiration. In the one, carbon dioxide is consumed, and in the other, it is liberated, but the assimilatory process is so much more rapid that it masks the respiratory process.

During the night, on the other hand, when assimilation is in abeyance, the respiratory process is unmasked. To demonstrate it, experimentally, it suffices but to shut off the light. If this be done and air deprived of its carbon dioxide be passed over leaves contained in the baryta-water apparatus (p. 60), the rapid clouding of the baryta water demonstrates the evolution of carbon dioxide. These facts are apparently the frail bases of the popular apprehension that it is deleterious to human health to keep flowers in a room at night. It is true that the flowers by night evolve carbon dioxide, but it is no less true that the amount of the gas which they give out is negligible and without influence upon even the most delicate person, waking or sleeping, who inhales the air of the room.

It may be added that the respiratory process common to all living cells, whether plant or animal, is generally far slower in plants than in animals. Only in active embryonic tissues, and among certain vigorously growing fungi and bacteria, does

respiration in plants attain to the magnitude that it reaches in animals. One explanation of the generally more sluggish respiration of plants is suggested by the fact that the higher, warm-blooded animals have heavy work of heat-production if they are to maintain body temperature at a fairly constant level.

The yeast plant has proved so valuable in elucidating the nature of respiration that it deserves a little further study. In order to increase and multiply, yeast, like any other plant, must acquire not only energy but material. The energy it gets by respiring sugar; but not all the sugar with which it is supplied is used in this way. Some is applied to constructional work. Nitrogen it also obtains from the nitrogen-containing substances, as, for example, ammonium tartrate, which occur in vegetable debris in which yeasts live. Carbohydrates, nitrogen compounds suitable for the synthesis of proteins, and essential mineral substances serve it no less than any other plant-cell for purposes of nutrition.

Once the significance of alcoholic fermentation is understood, that of many other kinds of fermentation becomes intelligible. Almost any naturally-occurring substance of which the oxidation, or even the splitting, results in a liberation of energy may be used by one micro-organism or another as a source of power. If only it is able by the agency of appropriate catalysts to unlock the stores, the organism has at all events the wherewithal to live. It must of course also obtain material for constructional purposes; but the debris of life is plentiful, and in it enough nitrogen and other essential materials occur in sufficient quantities to permit of the growth and multiplication of the world of micro-organisms.

The 'Open sesame' to membership of the lower world of non-green, saprophytic plants is the possession by would-be entrants of a respiratory catalyst or other power of extracting energy from this or that commonly-occurring, generally organic, substance produced by the wastage of dead things. Each and every substance rich in energy which abounds where

things live and die is to some one micro-organism its world—an oyster to be opened by its catalytic sword. Not until the energy-releasing process is complete and the raw material for its power-production exhausted does an organism in possession give way to successors which, in order to make good, must have the art to use as their meat the waste-products or leavings—poisonous, or at least unusable, to the predecessors which produced them.

So by many routes may the decadence of organic wastage of life be followed. Sugar may be oxidized once for all by any animal or plant-cell to carbon dioxide and water. Yeasts may split sugar to alcohol and carbon dioxide. Acetic acid bacteria, which turn wine into vinegar, may transform alcohol into acetic acid. Another yeast-like micro-organism, *Saccharomyces mycoderma*, may convert acetic acid into carbon dioxide and water. So by one vigorous turn, or by three successive turns, the wheel of change comes full circle, and the energy sent to the world by the sun is distributed to any organism apt to take it.

Of fermentation-like processes one of the most remarkable is that carried on by the nitrifying bacteria (see p. 89). The material which they 'ferment' is in the one organism ammonia, and in the other, nitrite. The oxidation of the one or the other releases energy whereby the organisms live, and it may be that the energy so obtained also serves nitrifying bacteria as a substitute for sunlight, enabling them to synthesize carbon compounds from carbon dioxide and water.

In no way is the versatility of life more manifest than in the variety of materials out of which plants are able to extract the substances necessary for the construction of their bodies and for the release of energy. Misery makes strange bed-fellows, and the struggle for existence, which no living organism may avoid, constrains many plants to specialize in energy-production from most unlikely materials. In consequence of this specialization, decay becomes orderly. No sooner has life left it than a body becomes the seat of operation of gangs of well-

disciplined, microscopic house-breakers. Each does, or rather undoes, his bit: breaks down some constituent of the once living body, and having done it that organism rests from its labours, for its supply of food and energy is gone. An Amurath, an Amurath succeeds! The waste-materials left after the work of the pioneers is finished serve as a source of material or power for their successors, and so on until the dead remains are at last dissipated throughout the world in the form of water, carbon dioxide, nitrogen, and mineral substances. By the sum total of their efforts these scavengers of Nature make the world habitable.

> For nought so vile that in the earth doth live
> But to the earth some special good doth give.

One of the most interesting conclusions to be drawn from a review of the modes of life of bacteria and fungi is that, whereas by far the larger number of species is saprophytic or parasitic, some—as, for example, the nitrifying bacteria—are as self-supporting as is the green plant itself. It is indeed probable that the kinds of non-chlorophyllous organism which are self-supporting—that is, capable of synthesizing their organic food-materials from inorganic compounds—are more numerous than is as yet generally supposed. Certain sulphur-bacteria, which play a part in keeping up the circulation of sulphur from the inorganic to the organic world and back again in continuous cycle, are apparently capable, like nitrifying bacteria, of living in media lacking organic matter. So it would seem that the great group known as bacteria contains not only forms which have fallen from high chlorophyllous, independent state to saprophytic or parasitic dependence on products of the synthetic activity of the green plant; but that it may contain also primitive forms of life capable of maintaining existence in the absence of the green plant, or even of sunlight. For all that is known, these organisms may be survivors of a world of life which existed even before the appearance of the first green plant.

The line of demarcation between the self-supplying or, as it is called, autotrophic plants, and the non-self-supporting, heterotrophic plants is not, however, clear-cut; micro-organisms exist which are apparently dependent on organic compounds for supplies of carbon, and yet able to make use of inorganic sources of supply of nitrogen. The nitrogen-fixing bacteria which live symbiotically in the roots of leguminous and certain other plants are examples of plants which are autotrophic with respect to nitrogen, and heterotrophic as regards carbon. There is, indeed, good reason to believe that the nitrogen-fixing nodule-organism (Fig. 13) derives supplies of carbohydrates from the tissues of the root in which it occurs. It is known, moreover, that other nitrogen-fixing bacteria exist which live a life untrammelled by symbiotic entanglements with higher plants. Free-living, nitrogen-fixing bacteria occur widely distributed, both in fertile soils and in the sea, and by their activity the sum total of organic compounds available for use by the higher plants is augmented. They bring the free nitrogen of the atmosphere into combination, build up their bodies, increase and multiply, and, dying, bequeath their organic remains to the world at large. One species of free-living, nitrogen-fixing bacteria—*Clostridium pasteurianum*—presents the paradox of an anaerobe which lives in the upper layers of the soil to which, of course, atmospheric oxygen has free access. It thrives only in the absence of oxygen, and yet lives surrounded by an abundance of that element. The truth is that *C. pasteurianum* lives in company with other micro-organisms which are so avid of oxygen that they use all that is available, and in the dearth of oxygen which they create the anaerobe thrives. In these conditions *C. pasteurianum* sets up vigorous fermentation of sugars released from the dead bodies of soil algae, &c., and uses the energy so derived for the synthesis of organic nitrogen-compounds. Among other nitrogen-fixing bacteria are species of *Azotobacter*, which live aerobically, some on land and some in sea.

As in ancient time all those who were afflicted and all those who were distressed found refuge in the cave of Adullam, so all along the evolutionary route followed by the green plant are to be found plants which have straggled from the ranks and, falling from the grace of greenness, have become saprophytes or parasites. Thus the fungi, of which vast numbers exist, are an evolutionary side-branch of the algae or of the ancestors of algae. There are also members of the fern alliance, *Pteridophytes*, e.g. certain Lycopods, which live at all events part of their lives as saprophytes—and there are many saprophytic, semi-parasitic, and wholly parasitic plants, which are undoubted members of the highest group of all—the Flowering Plants. No matter how strange and degenerate their bodies may be, they betray when they blossom their relation with flowering plants. Nor, after all, is it surprising that saprophytism and parasitism should accompany the green plant in its evolutionary progress, as faithfully as shadows accompany those who walk in the sun. For the green plant itself, both in its primitive and highly organized forms, shows saprophytic proclivities. Although, as water cultures indicate, a flowering plant may come to full maturity when supplied with carbon dioxide, water, and mineral substances only, yet if opportunity occur—if, for example, one or other of a great variety of organic nitrogen-compounds comes within range of its roots—the green plant may absorb and utilize it, and doubtless thrive all the better in consequence of its saprophytic exercise.

So it was in the beginning. Chlamydomonas, our example of the independent, unicellular, green plant, falls readily into saprophytic ways. Certain species, if organic nitrogen-compounds be plentiful, settle down on them, withdraw flagella and eye-spot, round themselves off, lose chlorophyll, and become colourless. In this state each cell grows and divides, until within each mother-wall a group of colourless cells is formed. The growth and division may be so great and frequent as to give rise to a colony of colourless cells all

lying in a mucilaginous envelope. Then presently, perhaps when the organic food-material begins to fail, the cells abandon their Capuan ease, develop chlorophyll, eye-spot, and flagella, and by lashing movements wriggle out from the mass of mucilage and become free, active, independent, and autotrophic again. Owing doubtless to their power of absorbing waste nitrogen-compounds, some species of Chlamydomonas become associates of the tissues of certain animals, and increase and multiply there until the animal, which in itself is colourless, becomes as green as any leaf. Such is the case with the minute Flat-worm, *Convoluta rosscoffensis*, which grows up only if it becomes 'infected' with a certain species of unicellular, Chlamydomonas-like, green alga. Many other instances of symbiotic relationship between green alga and animal are known, and are described in the author's little book entitled *Plant-Animals*.

Parallel with these examples of symbiosis are those furnished by the Lichens, in each of which an alga and a fungus live together in close association.

Saprophytism in flowering plants may take many forms. The Scotch pine and most of our broad-leaved trees also—beech and oak and birch—rarely, if ever, live absolutely independent lives. In natural conditions their roots are covered each with a fungus mantle, the matted hyphae of which, leaving bare the tip, spread over the growing region and dip between the walls of the surface cells. On roots thus infected root-hairs are not formed. Hence it is certain that the fungus absorbs water and mineral salts and passes them on to the root, but whether it does more is not known. In other cases the relation between flowering plant and fungus is closer and more intimate, and particularly is it so in not a few saprophytic plants, the yellow bird-nest, *Monotropa hypopitys*, and the brown bird-nest orchid, *Neottia nidus-avis*, of beech and other woods. In these more intimate associations between fungus and flowering plant the former penetrates into the living cells of the root and other underground parts. Therein it may be seen

sometimes growing vigorously, and sometimes fading away as the host-cells digest it. Strangest of all symbioses is that which obtains between certain species of fungi and epiphytic orchids. An orchid whose only lodgement is on the branch of some tree would naturally be expected to ensure the life of the species by producing many seeds, for otherwise chance and the wind could not guarantee their transport to a suitable harbourage. If many, the seeds would inevitably be small. They are, indeed, among the smallest—dust-like. But no one, not even the keenest seeker after adaptations, would have suspected what is indeed the case, that the seeds of orchids of this type do not contain a recognizable embryo at all. Within the narrow confines of the seed the future plant is represented in the most rudimentary fashion by a small group of cells. Not until ' good ground ' has been reached by the seed and infection by the fungus has occurred, does the puny embryo begin to become of recognizable plant-like form. Step by step as the young plant grows the fungus invades the tissues, never, however, extending throughout the plant, but keeping to the root and lower part of the shoot. The difficulties which orchid-growers used to experience in germinating certain species were in large measure due to ignorance of these facts, and to failure to secure the indispensable fungous partner. Some dim suspicion of the situation, or else some chance observation, led raisers of orchids to chop up bits of old root of the mother-plant and add them to the seed-bed. Now, with knowledge of the facts, growers may procure cultures of the fungus which frequents the roots of a given species and inoculate the seed-bed with the culture. What the fungus does beyond undoubtedly acting as an *Egeria* of growth is not known with certainty. There can be little doubt, however, but that it is concerned with the solution of the nitrogen problem—that problem of cosmic shortage of suitable nitrogen-compounds which has vexed the lives and affected the habits of plants throughout the course of their evolution.

Among no plants has the precariousness of the natural

supply of nitrogen given rise to stranger developments than it has among insectivorous plants. These plants include the sundews; for example, *Drosera rotundifolia*, found in boggy land in Britain, and other kinds of Drosera, *Dionaea muscipula* (Venus' fly-trap), and other genera of Droseraceae to the number of 100 species scattered all over the world. They include also the pitcher plants, the Nepenthes (Fig. 34), which frequent marshy places in the tropics of the Old World, and the Sarracenias of the New. By one device or another the insectivorous plant attracts, captures, and digests flies and such-like insects. In the simplest of them the insects are trapped and die. Time and decay set free from the dead captives nitrogenous substances of which some may be absorbed by the plant. In the more elaborate insectivorous plants—Drosera, Dionaea, and Nepenthes—proteolytic enzymes are excreted which aid in the dissolution of the bodies of entrapped insects and liberate amino-acid compounds which are absorbed by the living cells of the entrapping leaves.

There can be little doubt but that the insectivorous plants, though they may live without it, flourish, flower, and fruit far better when supplied with a meat diet. As good green plants they are autotrophic with respect to carbon. By depriving them of flies and other insects they may be made autotrophic with respect to nitrogen; but in Nature they derive accessory supplies of nitrogen and possibly also phosphates and other mineral salts by turning the tables on the animal world.

Other parasites obtain supplies from the living tissues of their hosts. Not always, however, does the parasite surrender wholly its autotrophic mode of life. The mistletoe (*Viscum album*), for example, keeps its chlorophyll and synthesizes carbon compounds like any other green plant. The suckers which it sends down into the living tissues of its host pass by the bast and make vital connexion only with the wood. Thereby the parasite obtains water and mineral salts, and doubtless when the sap rises in the tree it takes toll also of any organic substances which pass along the vessels.

FIG. 34. *Nepenthes Ratcliffiana*. Photograph by Malby.

FIG. 35. Broom-rape (*Orobanche minor*), parasitic on clover.

Not dissimilar in semi-parasitic state are species of *Pedicularis* (louse-wort). Above ground their green leaves give to them an air of independence: but below, their parasitism is revealed by the roots, which, when traced out, are seen to be attached by suckers to those of neighbouring plants. The broom-rapes, on the other hand (see Fig. 35), have abandoned themselves entirely to a parasitic habit. In their brown bodies there is no chlorophyll, and all their sustenance comes from the plant to which their roots are attached.

Any one who visits Land's End in summer may see the evening landscape of the moorland near the sea suffused with a dusky reddish glow. It is the dodder on the gorse. This parasite (Fig. 36)—of which there are numerous species, each attendant on one kind, or at most but few kinds, of plants—has an almost world-wide range. It pesters the British farmer by attacking his clover, and worries the seedsman because the seed of the dodder is very like that of clover. Other species may be met with twining about plants in the jungles of Ceylon: a

FIG. 36. Dodder (*Cuscuta europaea*), parasitic on the common tansy (*Tanacetum vulgare*)

widespread parasite indeed. The dodders are dedicated to a life of parasitism from their youth up, and their every activity is bent to the efficient discharge of their life-work. The young dodder is not as other seedlings are. It emerges from the seed as a pale yellowish, slender, almost thread-like seedling; wastes no time in root development, or in the formation of more than the minutest scale-like leaves; but grows ever longer, rearing its stem-end snake-like in the air, and coiling round in slow spirals almost like a cobra about to strike. When the spiral movement brings it to a host, the stem of the dodder twines about it like a tendril. If the host be of a suitable kind the coils tighten, but if not they relax and the spiral wandering through the air is resumed. With the tightening of the coils there grow out from the dodder suckers which penetrate the tissues of the host-plant. Within the suckers are bast and wood, and, as they penetrate, the bast comes in close connexion with that of the host, and the wood of the sucker joins likewise with that of the host, and, through wood and bast, the dodder sucks the verdure out of it. Thus the parasite thrives and the host declines. Should the decline come soon, before the dodder is ripe to flower, the still growing end of the parasite may cast loose again and resume its spiral growth. In this phase a yellower, almost greenish-yellow, colour may steal over it—a token of its once green state. Meeting another host the belated development of chlorophyll is foregone and the pale coils form once more. Not until it flowers would this strange plant be judged to be like any other, yet when blossom-time arrives it shows itself to be a flowering plant nearly related to the convolvulus.

Less exceptional in form, but no less completely parasitic, are the broom-rapes, species of which grow, some on ivy (*Orobanche hederae*), some on clover (*O. minor*) (Fig. 35), and others on other kinds of plants. With its sturdy, succulent, brown flowering-stem, the broom-rape, once seen, is not forgotten. Only when near to its host does the minute seed germinate. As soon as the seedling root is formed it becomes

attached to that of the host, and thenceforth all supplies of food come to the broom-rape from the roots to which it has affixed itself. So copious are the supplies they get that the broom-rapes form large heads of flowers, and the ripe capsules contain innumerable seeds. The broom-rapes are no doubt older at the parasitic trade than is the dodder, for their flowers, although not unlike those of pale, immature snapdragons, are nevertheless so distinct that they are placed in a Natural Order by themselves.

So like one who set out to climb, but having gone part of the way turns back, adding one more stone to the cairn of the unaccomplished, the dodders and the broom-rapes went all the long way of evolution from primitive to green flowering plants, only at last to fail of independence.

VII

The environment of the land plant: water-supply and sunlight. Stomata as regulators of gaseous exchange. The mechanism of stomatal movement. The role of transpiration in the economy of the plant. The transpiration stream (ascent of sap).

When benthic plants forsook the sea and became land plants they must have found the conditions of their new environment both strange and difficult. The holdfast organs which had served to attach them to the substratum might serve also to fix the land plant in the soil. Burrowing therein, the root-end would escape the heat of the sun, and in course of time might evolve the elaborate root-system which the higher plants of to-day possess. But for the stem-end there was no escape from drought or the heat of the sun. Even though it lay prostrate close to the surface of the ground, the aerial part of the plant must still suffer exposure to the elements. If it stood erect and grew upward toward the light, as most land plants do, although the leaves would be in better case to manufacture food-materials, every upward advance would increase the risk of desiccation. Unless therefore the migrants from the sea could evolve means of protecting their delicate yet necessarily exposed surfaces, conquest of the land was doomed to failure. They might survive here and there in moist, shady places as pygmy races of the lower orders, but they could never inherit the earth and the fullness thereof.

How the immigrants met and surmounted the strange and difficult conditions of their new environment, though it may never be known with certainty, may be conjectured. One of the first steps must have been the formation, out of the vast chemical resources of protoplasm, of a cutin-like 'water-proofing' material, and the deposition of it in, and on, the

surfaces of cells exposed to the air. So reinforced, the outer cell-walls became possessed of a high degree of imperviousness to water-vapour. As a peeled apple exposed to the air dries more rapidly than does one with its skin intact, so, and for the same reason, any cells with cuticularized walls lose water less rapidly than do those with walls of cellulose.

But a layer of cutin is no less effective in excluding carbon dioxide from the plant than it is in preventing the evaporation of water-vapour from it. So it would seem that the plant's landward course lay between the Scylla of desiccation and the Charybdis of starvation : for, without carbon dioxide, photosynthesis ceases and green plants languish and die. The course was safely steered. An epidermis was evolved which by the cuticularization of its outer cell-walls greatly impedes the diffusion of carbon dioxide and water-vapour from it, and at the same time provides definite channels through which diffusion may go on freely. These channels are the stomata (Fig. 16, p. 64). The more effective, however, are these means —and how effective stomata are in facilitating diffusion has been described already (p. 66)—the more the plant would appear to be once again at the mercy of drying winds or hot suns ; for if carbon dioxide may diffuse rapidly through stomata from the atmosphere into the plant, so may water-vapour diffuse from the air of the saturated intercellular spaces of leaves through the stomatal apertures and thence into the atmosphere.

The disastrous effects of a hot sun and dry soil may be observed when such a plant as the Royal Fern (*Osmunda regalis*), grown in a pot in a greenhouse, is brought into the open on a hot, sunny day. As the soil becomes dry the fronds wither, turn brown, and die. Microscopic examination of the fronds shows that the stomatal apertures are large and conspicuous. Through them diffusion of water-vapour goes on so rapidly that when supplies from the root begin to fail, desiccation and death of the fronds take place. Most plants, however, are far less readily injured by exposure to con-

ditions which bring about simultaneously a drying of the soil and an excessive loss of water from their leaves. If, for example, the experiment with the Royal Fern be repeated with almost any hardy pot-plant—a pelargonium, for example—it is found that, although the soil exposed to the warm air of a summer day becomes dry, and although the leaves may droop and the young stems wilt, the plant rarely suffers permanent injury. After the heat of the day has passed, a copious watering causes the stem to rise up again straight and supple, and the leaves to spread themselves, refreshed and green once more.

Microscopic examination of thin strips cut or torn from the surface of a leaf in a wilted condition shows that the stomatal apertures are scarcely to be seen—so small they are. Similar sections, prepared like the former by dropping thin strips as fast as they are cut or torn from the surface into absolute alcohol to prevent change occurring before the sections may be examined, if taken from unwithered leaves, show that the stomata are large and patent. In the case of the Royal Fern, on the other hand, no difference of size of the stomatal apertures of fresh and withering leaf is to be observed. It is evident therefore that, of plants which exist to-day, some possess the power of changing the size of their stomata; others, of which the Royal Fern is an example, accustomed to live in perpetually moist ground, lack the power. Inasmuch as movable stomata are found in all the higher divisions of the vegetable kingdom—mosses, ferns, and flowering plants—it is certain that the mechanism for stomatal movement was evolved early in the history of land plants, and proved so useful that it was retained by all higher plants save only some of those which live in moist and sheltered situations. These exceptional plants, though they retain stomata, have lost by disuse the mechanism which moves them.

The agents which bring about the opening and shutting of stomata are the guard-cells (see Figs. 16 and 37). They

operate osmotically. As with any other cells, when osmotic substances increase in the cell-sap of the guard-cells an increased osmotic pressure is developed. If water is available it passes osmotically into the cells, and with the increasing volume of the cell-sap the cell-walls become stretched. The cells increase in size. Unlike most cells, however, the guard-cells do not possess walls of uniform thickness, and, in consequence, the stretching of the walls which accompanies the absorption of water following on increase of osmotic pressure is not uniform. The thickened parts of the walls are less extensible and stretch less, and the thinner, more extensible parts stretch more. In the simplest type of stomatal mechanism, which occurs in certain mosses and in some flowering plants, the back part of the wall—that is, the part away from the stomatal aperture—is thickened, and the upper part of the wall may also be thickened. The cell-cavity which contains the cell-sap has a somewhat elliptical contour, with the long axis parallel to the free surface of the guard-cells (Fig. 37). As osmotic pressure rises in the guard-cells and water enters, the contour of the cell-cavity of each guard-cell becomes more spherical owing to the ' giving ' of the thin basal wall. In consequence of the movement, the walls bounding the stomatal aperture, previously closely pressed against one another, become straightened and in straightening separate. The stoma opens. If and when the osmotic pressure of the guard-cells decreases, water diffuses from the cells and the walls previously stretched are relaxed. The walls bounding the stomatal aperture, each resuming its curved contour, approach one another until the stomatal pore is obliterated: the stoma closes.

The power possessed by the guard-cells to change the osmotic pressure of their cell-sap depends on the presence of chloroplasts in the cells. Alone among the epidermal cells of ordinary land plants, the guard-cells possess green, chlorophyll-containing plastids. Other epidermal cells, though they

possess colourless plastids (leucoplasts), contain no green pigment. Hence when a leaf is exposed to light and its other green cells start into photosynthetic activity, the guard-cells begin likewise to photosynthesize. As a result of photosynthesis sugars are produced and stored in the cell-sap. But as shown already, sugars are osmotic substances, and therefore, with the accumulation of sugars in them, the guard-cells develop an increasing osmotic pressure, which leads to the opening of the stomata. It follows from the nature of the stomatal mechanism that two conditions are necessary in order that the mechanism should operate. For a stoma to open there must be an increase of osmotic substance in the guard-cells—that is, an increased power of absorbing water—and there must be also water available for absorption. For a stoma to close there need only be a fall of osmotic pressure in the guard-cells. Inasmuch, however, as all the cells of a leaf are organically connected with one another the closure of a stoma may be brought about as a consequence of competition for water between the cells. If, for example, the cells of a leaf lose water faster than they acquire it from the vessels of the veins, their osmotic pressure rises, and water may pass osmotically from the turgid guard-cells to the neighbouring cells.

The closure of stomata may come about in another way. As the green cells of the leaf may store surplus sugar in the form of starch, so may the guard-cells. If, therefore, from one cause or another, the sugar photosynthesized by the chloroplasts of the guard-cells becomes converted into starch, the osmotic pressure of the guard-cells falls; the cell-walls relax, water is excreted from the guard-cells, and the stoma closes.

The routine behaviour of stomata becomes intelligible in the light of these facts. The mechanism of movement of the guard-cells is automatically set going by any external or internal change which affects either the osmotic pressure of the guard-cells or the supply of water to them. Light, by

admitting of an increase of sugars in the guard-cells, initiates a train of events which results in the opening of the stomata. Darkness, on the other hand, brings about—at all events in many plants—closure of the stomata. With darkness photosynthesis ceases, the sugar of the guard-cells is either

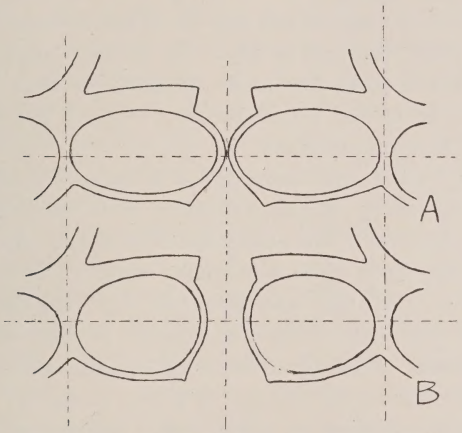


TABLE OF APPROXIMATE MEASUREMENTS.		
	CLOSED	OPEN
TOTAL LENGTH OF STOMA	50μ	50μ
TOTAL WIDTH OF STOMA	40μ	40μ
WIDTH OF ONE GUARD CELL	20μ	17μ
WIDTH OF FRONT CAVITY	9μ	9μ
WIDTH OF OPENING	0	6μ

FIG. 37. Guard-cells of a stoma. A, stoma closed; B, stoma open. (Adapted from Haberlandt.)

stored as starch or translocated from the cells, osmotic pressure falls, and the stomata close. Moist air favours the maintenance of the open condition. With plenty of water-vapour in the air the loss of water from the leaf is relatively little. There is, therefore, no lack of water for the guard-cells. They remain turgid and distended, and the stomata remain open. But if the air be very dry the loss of water from the green cells of the leaf is great: so great, indeed, that the

water rising from the root may be insufficient to keep them turgid. As the general cells of the leaf lose water, their osmotic pressure comes into operation, so that even though the stomata did not close by reason of their loss of water to the dry air of the stomatal space, they would have to do so because the increasingly acute competition for water between all the cells of the leaf would deprive them of water. Stomata close also when the soil is dry; for in this condition water-supplies become more and more deficient, so that the guard-cells presently losing water cannot replace it: their walls relax, and the stomata close.

For these reasons the stomata, at all events those of many kinds of flowering plants, exhibit a diurnal movement. At sunrise, or even before, they begin to open. As the morning wears on, they open yet more widely. If the day be not too hot, and the soil not too dry, the stomata remain open until the early afternoon. Before sunset they begin to close. Closure, completed in the early hours of the night, persists until the day is about to dawn: as though through long exposure to alternating change of conditions of light and darkness the plant has learned to anticipate them by rhythmic changes of its stomata. Yet at any moment force of habit may be overruled by force of circumstance. Drying winds or drought or removal into a dark place may bring about closure. To demonstrate closure resulting from undue loss of water, it suffices to cut off a broad delicate leaf and let it lie in the sun. As or even before the leaf withers, its stomata close. They may be caused to open again by syringing the leaf or immersing it in water. In not a few cases when stomata have been made to open in this way they fail to close again when the water has evaporated. So by giving a little water the death of the plant may be hastened; for it is manifest that the rate of loss of water through the stomata, and hence the desiccation of the leaf, is the more rapid the wider open are the stomata. It is this curious behaviour exhibited by not a few plants that sanctions the gardener's

aphorism, ' A little water is a dangerous thing '. It sanctions also the practice of good gardeners both in not watering too soon and in watering copiously when they are compelled by circumstances to begin.

With the closure of stomata, photosynthesis comes to a standstill, and remains at a standstill until the stomata open again. That the cause of the cessation of manufacturing activity is the shutting off of supplies of carbon dioxide has been suggested already (p. 77), and may be demonstrated by so treating a leaf that, in despite of its stomata being closed, carbon dioxide reaches the green cells. This may be done by plucking a leaf in the early morning before it has produced starch, and exposing it to dry air until the leaf begins to wither. If, as usually happens, the stomata close, starch does not accumulate in the leaf. Yet if—as, for example, by puncturing the surface with a fine needle—diffusion of carbon dioxide into the leaf is rendered possible, starch soon appears in the green cells neighbouring on each puncture—a proof that, with renewed supplies of carbon dioxide, photosynthetic activity is possible even in a partly withered leaf.

The automatic shutting down of manufacturing activity which follows on stomatal closure is no disadvantage to the plant. In darkness photosynthesis ceases whether the stomata close or not; there are, indeed, circumstances in which a real and great advantage may accrue to the plant owing to its habit of stomatal closure. During the night the root continues to absorb water and mineral salts and any tissues which may have been deprived of water owing to excessive transpiration during the previous day are able to replenish their stores and to become turgid and ready for the next day's work. In some plants, indeed, the absorbent activity of the root during the night may be so great as to provide water not only for the relatively small amount transpired by a leaf in darkness with closed stomata, but also enough, or even more than enough, to restore full

turgidity to the tissues of stem and leaf. When it happens that the water absorbed during the night is more than enough for these purposes, the excess may be excreted and appear as dew-like drops on the tips or edges of the leaves. A field of oats or a greenhouse full of Chinese primulas may thus present a very beautiful appearance in the early hours of the morning, each leaf bedewed with shining drops of water. In some tropical plants, e. g. species of *Colocasia*, so much water may be excreted that each leaf sheds wellnigh 200 drops a minute, so that the fanciful may imagine that floods of tears are falling. The nectar which is found in the spurs or other parts of many kinds of flower is produced in a not dissimilar manner. The glandular cells of the nectary liberate sugars which accumulate on their outer surface. When the cells of the nectary are so fully supplied with water that they become turgid, the sugar outside withdraws water osmotically from them, with the result that drops of sweet nectar accumulate in the nectary.

The cessation of photosynthesis following on stomatal closure due to dry air or soil is but one manifestation of the fact that unless cells are adequately supplied with water they cease all vital activity. Moreover, by stomatal closure the plant tends to avert the fatal danger of insufficiency of water; when it is either getting too little or losing too much it is clearly time to cease work, for though work may be the most important thing in life, work without health is of no avail. Thus the stomatal lock-gates of the leaf, by shutting off or promoting the diffusive flow of carbon dioxide and water-vapour to and from the plant, provide means whereby land vegetation meets and overcomes difficulties inseparable from a terrestrial existence. They confer on the green plant some measure of mastery of its fate. The limitations and extent of the mastery are revealed to any one who will watch young plants overtaken by a spring drought soon after planting. Those which have not had time to get a good root-hold succumb, but plants the roots of which have made

such growth as to be secure of some supplies of water, however meagre, may withstand the drought. Leaves may hang distressfully and idle, and the plants may remain inert with growth at a standstill for weeks; yet, when the rains come, many recover, and, though some are permanently stunted and flower prematurely, most of them are none the worse for the ordeal and live to a green old age.

That the possession of stomata may at times prove a source of weakness to the green plant is only to be expected in a world of such varied conditions as this is. Certain parasitic fungi (for example, those which produce blight of potatoes and rust of wheat, which cause immense annual losses) gain access to the tissues of the plant through the stomata. Were it not for the stomata, stems and leaves might prove invulnerable to attack, for the spores of the blight and rust fungi, which germinate on the moist surface of the leaves, are unable to penetrate the cuticle even of the seedling plant. The open stomata, however, offer innumerable, sufficiently spacious and attractive routes along which the growing germ-tube of the germinated spore may travel and reach the moist intercellular spaces of the leaf. Thence the fungus penetrates the soft walls of the cells of the leaf, and spreading from cell to cell carries out its work of destruction as it goes.

This, however, is after all but a small matter to vegetation, albeit a large one to the farming community, for in despite of their prevalence, parasitic fungi have not been known to destroy completely any species of plant. Moreover, by no means all parasitic fungi which injure or destroy plants make their assaults through the stomata. Some gain entrance through punctures and wounds, and others have power to penetrate through the general epidermis, and so find their way into the host plant.

The disastrous effects on plants of the smoky atmosphere of highly industrialized districts provide another illustration of the incidental disadvantages which may attend the possession by plants of stomatal channels through which gases may

diffuse. The stomata may be blocked by the greasy tar-like products formed by the incomplete combustion of coal, or they may give passage to poisonous gases, to some of which—for example, coal-gas—plants are highly susceptible. Thus it is that in the neighbourhood of great industrial cities vegetation wears a dejected aspect, and autumnal colours—the sign of the end of the plant's working year—follow close upon the tender green of spring.

So much has been said of the importance of stomata in the life of the land plant that it may be of interest to describe briefly how the state of the stomata at any given moment may be ascertained, and how the effects of external conditions—light, atmospheric moisture, and supply of water—on stomatal movement may be demonstrated. An apparatus of simple construction, known as the Porometer (Fig. 38), serves for these purposes. It consists of a T-shaped glass tube, to one of the shorter limbs of which is attached a glass bell-jar, so small and light as to fit easily over part of the surface of a leaf. To the other short limb is attached a piece of thick-walled rubber tubing provided with a clamp. The long limb, behind which a scale is fixed, dips into water. The bell-jar is attached to the leaf by an air-tight junction, made by means of gelatine or wax of low melting-point. To use the porometer, suction is applied at the open end of the rubber tube until water has reached a given height in the long limb of the T-tube. The rubber tube is clamped and the rate of fall of the water column is recorded. If no stomata are present on the surface of the leaf attached to the bell-jar, the water column remains at its original height, for although, with the withdrawal of air from the apparatus, the pressure within the bell-jar is less than that of the atmosphere, the continuous epidermis prevents the passage of air through the leaf into the bell-jar. If, however, stomata occur on the surface of the leaf beneath the bell-jar, the difference of pressure between the air in the bell-jar and that outside leads to a diffusion of air from the atmo-

sphere through the stomatal apertures into the intercellular spaces of the leaf, and thence through the stomata under the bell-jar into the apparatus. As a consequence the water column falls, and goes on falling to the zero mark—that is,

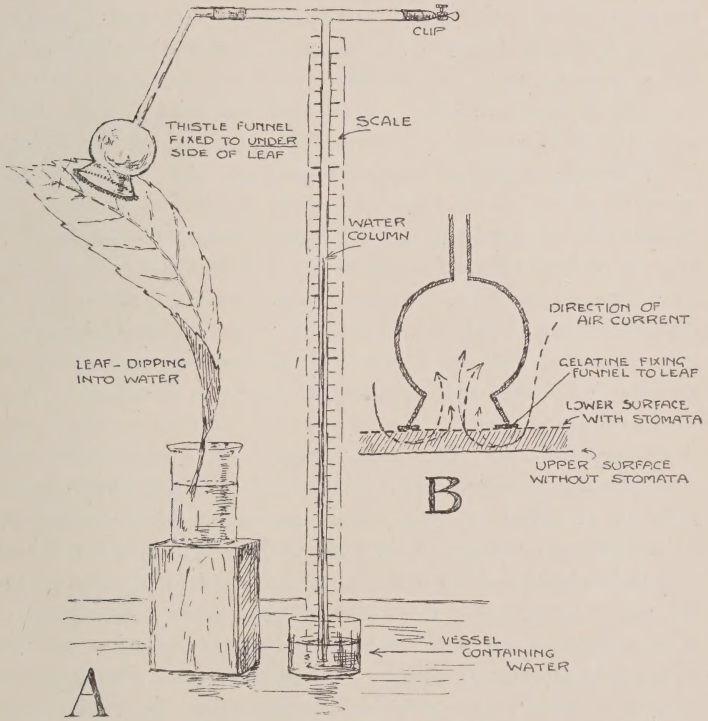


Fig. 38. Porometer (see text).

until the inner and outer atmospheric pressures are equalized (Fig. 38 B). It stands to reason that the wider open the stomata the faster is the diffusion, and therefore the faster is the fall of the water column. Hence by making a series of readings first with the upper surface, and later with the under surface of a leaf attached to the bell-jar, the rate of fall

of the water column may be used to indicate the presence or absence of stomata, or their relative numerical distribution on each of the two leaf-surfaces. Similarly, by altering the conditions—for example, of illumination, dryness, or stillness of air—the effect of the alteration may be estimated by observing the change in the rate of fall of the water column. Simpler means may also be used to demonstrate that the state of the stomata determines the readiness with which gases or liquids may enter the leaf. The red anthocyan pigments of plants generally turn a greenish colour when acted upon by ammonia. If, therefore, a leaf of copper beech, or other similarly pigmented plant, partly covered with black paper until the stomata in the darkened part have closed, be exposed to vapour of ammonia, greening of the red pigment may be seen to occur rapidly in the illuminated part, and only slowly in the darkened part of the leaf. Or any delicate, similarly darkened leaf may be used to show that liquids—as, for example, alcohol—penetrate more rapidly when stomata are open than when they are closed.

To demonstrate the transpiration of water-vapour by stomata, advantage may be taken of the fact that certain salts—e. g. cobalt chloride—change colour when in contact with moisture. Strips of filter-paper dipped in cobalt chloride and dried have a blue colour. A strip is laid closely on the stomatal surface of a leaf, and covered with a thin glass or mica strip in order to prevent access of atmospheric moisture. A gradual change of colour from blue to pink indicates the escape of water-vapour through the stomata. If, on the other hand, the covered surface lack stomata, no, or at most a slow and slight, change of colour takes place.

Yet another very simple experiment may be used to demonstrate the fact that the rate of transpiration from a leaf depends on the state of the stomata. A pair of leathery leaves with stomata on one surface only—e. g. of the India-rubber plant (*Ficus elastica*)—are cut from a plant, and the ends of the stalks fitted each with a rubber tube, bent and bound

by wire on itself, in order to prevent escape of water-vapour through the cut ends of the stalks, and as a means of hanging up the leaves in a room. The lower surface of one leaf and the upper surface of the other are smeared with vaseline. In the course of a few days the leaf the lower stomatal surface of which was not coated with vaseline curls up and withers, whereas the other leaf—that in which the vaseline was used to block the stomata—remains fresh. By weighing the leaves at the beginning and end of the experiment it is found that whereas the withered leaf with freely exposed stomata has lost much, the other, of which the stomata were blocked, has lost but very little water.

In order to measure accurately the actual amount of water transpired by the leaves of plants, recourse is had to the weighing of pot-plants, but there is another less laborious method which may be used to give a measure of the rates at which leaves give off water. The method consists in timing the rate at which water passes along a very narrow glass tube, connected at one end with a water-supply and at the other with a glass vessel into which a leafy branch is fixed by an air-tight joint. The details of the apparatus—the potometer—are shown in Fig. 39. In order to measure the rate of movement of the water column two marks at convenient distance from one another are made on the narrow tube. When the cut end of the branch is placed in the vessel, which is completely filled with water, and all junctions made air-tight, the bent end of the narrow tube which dips in water is raised momentarily to admit of a bubble of air. The end of the tube is replaced in the water, and the time the air-bubble takes to pass from mark to mark is measured by means of a stop-watch. The mean of a series of readings gives the average rate of absorption of water by the cut end of the stem, and since, if suitable precautions have been taken, it is found that the rate at which water enters the cut end is equal to that at which water-vapour is given off by the leaf-surfaces, the rate of the movement of the air-

bubble may be used to obtain a measure of transpiration. Inasmuch as the apparatus is portable, it may be taken from bright light to shade or darkness and back again to bright light, and in this way may be used to demonstrate that the rate of transpiration of ordinary broad leaves is highest in bright sunlight, falls in diffuse light, and falls still more in darkness. Similarly, the potometer may be used to demonstrate the effect of wind produced naturally or by blasts from a bellows in accelerating transpiration; and in like manner the relative rates of transpiration in moist and dry air may be determined.

The precautions which must be taken if the potometer is to serve these purposes are: first, that the branch must be cut under water, and second, that after having been cut it must be kept with its cut end in water for several hours before measurements are taken. The reasons why these precautions are necessary are worthy of note, inasmuch as they throw some light on the problem to be considered presently, that of the state of the conducting woody vessels with respect to water. If the woody vessels of an active plant were permanently and completely filled with water there would be little need of the first precaution. But as a matter of fact the woody vessels are rarely filled with continuous water columns. At one time, perhaps, they may be—for example, after a still night in moist air. At other times, and particularly when transpiration is going on rapidly, the amount of water passing from the root into the vessels is not enough to replace that lost by transpiration, and as a consequence the vessels cease to be filled with water. They now contain both water and air, and the air, moreover, is under a pressure less than that of the atmosphere. It therefore follows that when a branch in this state is cut, and the cut surface is exposed, air passes rapidly into the vessels through the cut end of the stem, and continues to pass in until the pressure inside the vessels is equal to that of the atmosphere. Experiment shows that when the woody

vessels are blocked in this way by air, conduction of water up the vessels to the leaves is impeded. Hence without the precaution of cutting the branch under water the apparent rate of transpiration as measured by the potometer will

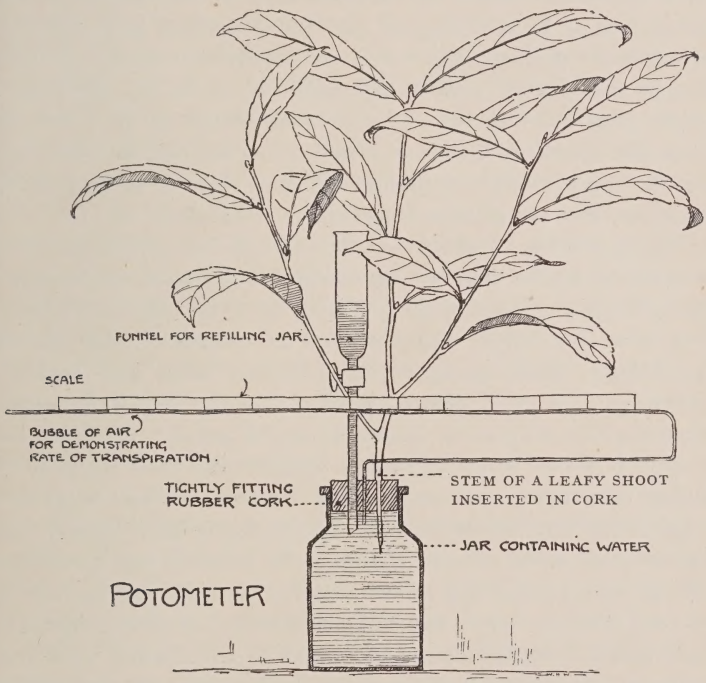

FUNNEL FOR REFILLING JAR.
SCALE
BUBBLE OF AIR FOR DEMONSTRATING RATE OF TRANSPIRATION.
TIGHTLY FITTING RUBBER CORK
STEM OF A LEAFY SHOOT INSERTED IN CORK
JAR CONTAINING WATER
POTOMETER

FIG. 39. Potometer (see text).

be at first much quicker and then slower than it actually is in the intact branch. For the same reason the branch is left in water for some hours before measurements are made; for during this time, if the vessels contain air under less than atmospheric pressure, water is being forced into the plant by atmospheric pressure, and until the internal and external pressures have been equalized the flow of water

along the potometer tube, due to atmospheric pressure, gives no indication of the actual rate at which water is being transpired by the leaves.

The rapidity with which water may be injected by atmospheric pressure into a cut branch may be demonstrated by immersing a branch during and after cutting in a watery solution of a dye—e. g. eosin or methylene blue. If the day be a sunny one and transpiration vigorous, the difference of air pressure outside and inside the plant is so great as to cause the water to rise so rapidly that the dye accompanying it may be found on slicing into the stem to have passed in a few minutes along a length of many inches.

When results obtained by the use of the potometer are considered in the light of knowledge of stomatal movement, two sets of apparently contradictory facts become reconciled. On the one hand, transpiration is facilitated by those conditions which promote evaporation from any watery surface. Just as clothes hung on a line dry better in warm than in cold air, so do plants transpire more; and just as drying is faster when the air is unsaturated than when it is full of moisture, so is transpiration. Indeed, the loss of water-vapour from the cell-walls abutting on intercellular spaces, the diffusion of water-vapour through the intercellular spaces to the stomatal pores and thence into the open air, are the result of evaporation. But, as has been shown, the plant, through its stomatal mechanism, has means of interfering with the process. By reducing or enlarging the stomata, the rate which would otherwise be maintained may be increased or reduced. There is also the further fact, not so clearly understood, that light appears to exert an influence on the rate of transpiration greater than would be expected if it operated merely by bringing about a change in the size of the stomatal apertures. For this, as well as for other reasons, it may be well to regard the loss of water by the cells of the leaf as not merely a physical but as a physiological process; and to regard transpiration as an excretory process. Looked at from this point

of view, what actually happens is what would be expected. In a general way those conditions which favour evaporation also favour transpiration : but the guard-cells may intervene, and by modifying the stomatal aperture alter the rate. Furthermore, the actual secretion of water by living cells, though doubtless determined by physical laws, may be influenced by conditions—as, for example, light—which do not affect evaporation. That this view is very likely correct is indicated by numerous facts. Submerged water plants may transpire water from their leaves, and land plants, although kept in a saturated atmosphere, manage to effect a certain amount of transpiration. In coal-mines, festoons of fungi hanging from the pit-props may be seen to excrete drops of water which shine in the semi-darkness like pearls.

In any case, whatever view be taken of the transpiration mechanism, there can be no doubt but that, as experiments with the potometer show, and every gardener knows by experience, the stream of water passing through the plant in the course of a growing season is very great. There are, indeed, good reasons why it should be. For, in the first place, the transpiration stream is the only means the plant has of concentrating adequate supplies of mineral salts in its leaves. The soil solution in which are the essential mineral salts is very dilute ; yet as shown in Table II (p. 45) leaves may contain large quantities of these substances, and thus it is that, as experiment shows, the rate of transpiration of a given plant is affected not only by light, dry air, and quantity of water available, but also by the amount of mineral salts contained in the soil.

Thus if equal numbers of a green plant be grown in plots of equal size in one and the same field poor in essential mineral salts, the rates of transpiration may vary widely according as artificial fertilizers, salts of nitrogen, potassium, and phosphorus are added to the plots or not. In the case of one such experiment with oats, it was found that whereas plants grown on the manured soil transpired 225 pounds of water for every

pound of dry matter they produced, those grown on unmanured but otherwise similar soil transpired no less than 260 pounds for each pound of dry matter they produced. No doubt the higher rate of transpiration in the latter case was rendered possible by a wider ranging and more developed root-system, but the fact remains that the rate of transpiration of a plant bears a relation to the amount of soluble mineral matter present in the soil, and thus is justified the view that the possession of the power of rapid transpiration secures to the plant means of obtaining from the very dilute soil solution a sufficiency of essential mineral substances.

The bearings of these facts on agriculture are worthy of note. Systematic use of artificial manures may both increase yield and enable plants to flourish in dry years or places when and where plants in an unenriched soil would succumb. There is, however, a strict limit beyond which a further increase of soluble artificial manures produces not only no beneficial, but actually an injurious effect. Many a farmer and gardener, encouraged by witnessing the growth of crops supplied with a dressing of nitrate of soda or sulphate of ammonia, has essayed to get yet better results by far more generous dressings. The result has been that his plants have been checked or killed. The soluble artificial fertilizers—nitrate of soda, &c.—are osmotic substances, and if they be added to the soil in excessive quantity may withdraw water from the root-hairs and thereby interfere with their activity, or else, entering the cells in excessive quantity, the nitrate or the salt of ammonia may act as a poison to them.

Yet another advantage accrues to a green plant from its power of rapid transpiration. By regulation of the rate of evaporation from the surface of the aerial parts, the temperature of the leaves is also regulated. The radiant energy absorbed by leaves exposed to bright sunshine would surely raise the temperature of the tissues to a dangerous degree were it not employed in large part in effecting the evaporation of water. Energy used in this way cannot be used in another, and so the

plant may escape injury. Moreover, as is well known, the surface from which evaporation is going on is cooled thereby —as witness the cool nose of a healthy dog, or the relative coldness of leaves fully exposed to the sun.

Even though the air become dry and the stomata close, the amount of water transpired, although reduced, is generally enough to exert a cooling effect sufficient to prevent the temperature, even of leaves exposed to full sunshine, from reaching the danger point. The nocturnal closure of stomata also operates beneficially ; with stomatic closure transpiration falls off, and there is less cooling, so that, as, for example, on cloudless nights when radiation of heat is great, the danger to the plant of an undue fall of temperature is, although not averted, lessened.

It is probable that herein lies the significance of the sleep movements exhibited by the foliage and also the floral leaves (petals) of many different kinds of plant. Sleep movements of foliage leaves are manifested by the runner-bean (*Phaseolus multiflorus*), sensitive plant, species of oxalis, &c. In the diurnal position the leaf-blades are spread out more or less horizontally, freely exposed to the air. When night comes the blades in some plants hang down, and in others stand up vertically, so that they transpire less water and radiate less heat. Each blade may also fold on itself, using the midrib as a hinge, or, in the case of compound leaves, each of which consists of numerous leaflets, e.g. *Mimosa pudica* (Fig. 49, p. 229), opposite leaflets may fold together in pairs.

It is evident that the nocturnal movement of leaves which exhibit sleep movement brings about a reduction of freely exposed surface, and hence a checking of transpiration and of radiation, and so—as, for example, on clear frosty nights in spring—sleep movements confer some measure of protection on the delicate tissues of the leaf. The need, on the other hand, for active transpiration and for avoidance of the risk of desiccation has compelled wellnigh every plant that grows to strike a compromise between efficiency of transpiration and

self-protection. Where, as in our country, the summer is temperate and the climate moist, trees and shrubs and herbs with broad leaves abound, and the compromise is little evident until winter comes. Then the broad-leaved trees shed their leaves altogether, for the soil is cold and winds are often strong, and to bear leaves would be to court disaster. Thus it is that our broad-leaved trees have compromised with climate. Their leaves live and work at high pressure during the short season, and are cast off when the summer is past. The vegetation under another climate bears a very different aspect. The trees and shrubs of the Riviera, for example, are for the most part evergreen, and many of them have leathery leaves, which are often—as, for example, in the cork oak (*Quercus suber*)—smaller and of a darker green than are those of our oaks and other trees. Living all the year round, the leaves must perforce be able to stand the hot sun of summer, and so evergreen trees native of the Riviera, with wellnigh twelve months in which to do their work, can afford to make the sacrifice of surface in the interests of security from desiccation.

Given a knowledge of the seasons and the soil of a country it is generally possible to hazard a shrewd conjecture of the kind of vegetation that occurs there : not of the actual kinds of plants which make up the flora, but of the general aspects which the vegetation presents. Consider, for example, some of the peculiar plants commonly grown in gardens or found native in England. The house-leek (*Sempervivum tectorum*), which is often planted on roofs and walls, and lives in Switzerland on alpine rock surfaces, bears close rosettes of fleshy leaves ; the gorse (*Ulex europaeus*), native of dry sandy commons, has spiny branches and the merest vestiges of leaves ; the pines have leathery needle-like leaves. It is evident that the succulence of the house-leek, the all but leaflessness of the gorse, and the leatheriness of pine leaves, all indicate a water consumption less than that of plants with broad delicate leaves. The broad-leaved tree with access to

plentiful supplies can afford to use water freely—light come, light go. These others—xerophytic plants—needs must economize it. The house-leek can get but little from the small parcel of debris on the rock to which its roots cling. The gorse and the pine growing in wind-swept places, and often in thirsty sand, are no doubt by nature, and also by force of circumstance, niggardly in transpiring water.

How the many diverse modifications of leaf- and stem-structure exhibited by different kinds of xerophytes have come about would of course be of great interest to explore. Here, however, it must suffice to show from the results of experiments how great and how diverse are the water requirements of plants. A broad-leaved herbaceous plant—a sunflower, for example—may give off a pint or more of water on a hot sunny day. If an apple-tree wilts in hot weather any one who seeks to restore it must need to pour about its roots not less than a hundred gallons of water. A beech tree on any day of summer transpires not far short of a hundred gallons. It is estimated that a well-grown oak tree, with leaves numbering three-quarters of a million, each with its millions of stomata, gives off during the five months of its active annual life more than 200 tons of water. The wheat plant, which is by no means a thirsty plant, transpires in its season of growth at the rate of 1,000 tons per acre ; that is, if it is to produce a crop, an acre of wheat needs must lift from the soil and evaporate from its leaves not less than the equivalent of ten inches of rain. Seeing that in our eastern counties, where much wheat is grown, the total annual rainfall ranges from 20 to 25 inches, and that much of winter rain drains away or evaporates unused by the plant, it is plain that water-supply must often act as a limiting factor to crop production even in our country, and that water it is which marks the bounds between ' the desert and the sown '.

Some measure of the magnitude of transpiration may be gained by estimating the total amount of water which the wheat crop of the world returns to the atmosphere. Taking the area under wheat (p. 41), as 400,000 square miles = 256

million acres, and allowing the average annual amount of transpiration to be equivalent to 1,000 tons per acre, the water transpired annually by the world's wheat crop is not less than a quarter of a billion tons. Yet other cultivated plants take far more water from the soil than does wheat. Clover, in order to produce a dry-weight yield equal to that of wheat, would require to transpire half as much again as wheat. Away at the other end of the scale stand the xerophytes—water economizers which perforce must be content with a relatively small amount of transpiration, either because they cannot get water fast enough for a quicker use, or because the evolutionary experience which they have passed through has led to such a reduction of transpiring surface and such other modifications of their tissues that they now, even when exposed to conditions facilitating transpiration, give off relatively little water. Thus it is with the succulent Cactaceae, which live chiefly in the dry deserts of sub-tropical and tropical America. The amount of water transpired under given conditions by one of the Cactaceae—e.g. the prickly pear, *Opuntia cylindrica* —compared with that given off in the same time by a broad-leaved plant, e.g. *Hydrangea* (*H. hortensis*), is astonishingly small, as the following records show. The amount transpired on a given day by a leafy shoot of *Hydrangea* weighing 100 grms. was found to be 236·2 c.c. (about half a pint), and that given off in the same time by an *Opuntia* of equal weight, 0·52 c.c., so that weight for weight the transpiration of the one is nearly 500 times that of the other. But the *Opuntia* are thick and fleshy (Fig. 40). Their bulk is great in proportion to surface. Even so, if the surface of the plants used in the above experiment be measured, it is found that the amounts of transpiration per 100 sq. cm. of surface are 6·54 c.c. in the *Hydrangea* and 0·20 c.c. in the *Opuntia*; that is, the rate of transpiration of the one is about thirty-two times faster than the other. With such a gearing down of the process, the Cactaceae are able to persist even in the inhospitable dry deserts of tropical America.

FIG. 40. Xerophytic plants naturalized in the Riviera. *Opuntia ficus indica*—native of American deserts—with the tall-growing, cylindrical *Cereus setispina* from the W. Indies

By its elasticity with respect to water requirements vegetation has consummated the conquest of the earth.

The high rate of transpiration exhibited by broad-leaved, actively growing trees cannot fail to suggest the question—by what means is the plant able to effect rapid movements of large quantities of water over distances so great as those which separate the absorbent organs of the root from the leaves of the topmost bough ?

The tallest trees of the world—*Eucalyptus* of Australia, for example—attain to a height of 300 feet. Their roots are also of great length, so that inasmuch as it is only the young part of roots which absorb water, the maximum distance over which water is transported in these and similarly tall trees can scarcely be less than two hundred yards.

This question, which is often referred to as the problem of the ascent of sap, has not even now received an answer which completely satisfies every one who has investigated it. Hence the explanation about to be given must be regarded as provisional and not final. In the first place, it has been shown that although absorption by the root only takes place when the absorbing-cells are alive, the transpiration current—i.e. the water current—may go on flowing through the woody vessels from root to leaf, even though a long section of the stem has been completely killed—as, for example, by steam or by the injection of poisonous substances. When, however, in the latter case the poison reaches and kills the leaves, the transpiration current ceases. The leaves receiving no more water, wither, and losing more and more water by evaporation, become dry and brittle. The passage of water from soil into the root-hair cells, and thence across the root to the young vessels, has already been attributed to osmotic pressure. No less than the root-hair cells—or, for that matter, any living vegetable cell—the green cells of the leaf, rich in osmotic substances, are capable of exerting very great osmotic pressures. Actual measurement has shown pressures so high as, and even in certain cases far higher than, thirty atmospheres, and needless

to say such pressures, if they could be applied, would suffice to lift a water column to the top of the tallest tree.

The problem therefore resolves itself into a study of the way in which the osmotic pressure of the cells in a transpiring leaf may be applied to the lifting of the long water columns in the woody vessels. It would be relatively easy to understand how this might be done if, when transpiration is most active, there existed in the wood-vessels continuous columns of water stretching from leaf to root. But observations of the wood of living, actively transpiring trees tends to show that when transpiration is active air as well as water occurs in the vessels. Sometimes water and air bubbles alternate. Sometimes not much more than mere films of water adhering to the walls are to be seen. If therefore the supply of water of transpiration is to be maintained—as in fact it is—water must rise in films or hollow cylinders between the air of the vessels and the walls. That a pull from above should result in a bodily lift of hollow cylinders of water is hard to believe or understand. Yet water has certain surprising properties which help to make this belief not impossible. A thistle funnel covered with parchment membrane, completely filled with water and stood with the lower part of its stem in mercury, may be used to demonstrate that the evaporation of water from the parchment membrane results in a rise of the mercury in the tube. Evaporation has exerted a measurable 'pull'. Before long, however, bubbles of air accumulate beneath the parchment membrane and the rise of the mercury ceases. If the experiment be repeated with the thistle funnel full of boiled water, the evaporation 'pull' results in a yet higher rise of the mercury. But again the rise comes to an end when atmospheric air breaks back and clogs the space between water and parchment membrane. When plaster of Paris is used instead of parchment a yet higher rise of the mercury column may be observed—so much indeed as 80 or more centimetres: a height greater than that (about 76 centimetres) to which mercury may be raised in a barometer by atmospheric pressure.

In these experiments the water particles or molecular aggregates cohere with one another, and adhere also to the mercury, in spite of the increasing weight of the mercury column which they hold up. Water, therefore, has power of cohering with water, and hence, if it could be shown that this power is sufficient to prevent the long and it may be hollow water columns in the woody vessels of actively transpiring trees from breaking, the problem of the ascent of sap might perhaps be regarded as solved. The root ensures the intake of enough water. The leaves supply the pull. Sometimes, indeed, the root does more than supply the water. It may force it into the vessels. A vine cut down in spring may be seen to bleed, and if a manometer be connected with the end of the stem the bleeding pressure may be shown to be considerable. This fact, however, does little in explaining the ascent of sap; for bleeding takes place in spring, and is often more in the hours of the night than it is in the day, whereas if the pressure which sets up bleeding were an aid to the ascent of water it might be expected to be most apparent in the summer and in the daytime. Nevertheless, root pressure may assist indirectly by helping to make good the reserve of water in the vessels of the root and lower part of the stem, and also by supplying water to living cells which may perforce have lost water during the day when the leaves were actively transpiring.

Somehow, then, the ascent of water is contrived and maintained; with the water go the mineral salts, which thus get quick transport to the leaves, for the ascent of water is a mass movement, and not a slow movement due to diffusion of molecules. In spring, sugars and nitrogen compounds stored during the previous summer in the living cells of the wood (wood parenchyma) are discharged into the vessels, travel in the ascending water current, and by this route rapidly arrive in the young leaves and growing stems. How these materials, originally manufactured by the leaves, reach the far-away tissues of stem, and even root, is not so clear. Many experi-

ments made by ringing trees—that is, removing the bark, &c., down to the wood—seem to show that the ' elaborated ' sap (sugars and nitrogenous compounds) passes by the way of the phloem. If it does so it is a very wonderful thing, for the rate at which the sugars and other synthesized food-materials pass from the leaf down the stem is relatively great, and the sieve-tubes, and indeed all the phloem elements, are narrow and relatively few. To send these materials along the phloem on their course to all parts of the plant would require some kind of activity at present not understood. The alternative has been propounded that the food-materials manufactured by the leaves, that is, the ' elaborated sap ', no less than the ' crude sap '—the water and mineral salts—travel along the vessels. If this were finally proved the nature of the plant's machinery for distribution would at last become clear and intelligible. In the mind's eye there might be seen in the woody vessels currents of water ascending in some and descending in others: ascending along certain tracts and descending along certain other tracts of vessels. At each step in the ascent or descent the cells bordering on the vessels would take toll of the materials they require. They would perforce share their acquisitions with other neighbouring cells, like themselves hungry for food-materials. The moving water currents would bring all things needful within range of all the tissues near the woody vessels. The cells of the tissues abutting on the vessels would obtain supplies from the passing stream, and the distribution to other cells would proceed from cell to cell by the slow but sure process of diffusion.

Thus the study of transpiration leads from the clear domain of the certain to the dimly uncertain, and beyond to the unknown, the darkness of which only future research may enlighten. Nevertheless, that which is known shows how great is the part which water plays in the life of the green plant, and with what versatility the plant has adjusted itself either to make use of water or to endure, even though there may be but little water of which it may make use.

VIII

Variation and Heredity: Evolution. Reproduction; asexual and sexual. Cell and nuclear division: the Chromosomes as the material bases of Heredity. The experimental breeding of plants and animals. Mendelian inheritance.

Of all life's manifestations none is more familiar or more wonderful than the perpetuation, generation after generation, of plants and animals, each after its kind. Generation succeeds generation, the new repeating the distinctive features of the old with such fidelity that each kind of plant and animal seems to be immutable. So alike, indeed, are the members of each several kind of organism that they are grouped together as a species, and are all known by the same name: for example, *Rosa canina* (dog-rose), designating by the specific name all dog-roses, and by the generic name all roses.

But though the passer-by may see no difference between the members of a flock of sheep, the shepherd and the sheep-dog do. So also those who tend plants and animals discover that the members of a species are by no means all alike. Not only are there differences between them, but the differences are of different kinds. Members of a species may be marshalled into groups, any one of which exhibits it may be slight, yet, nevertheless, constant differences from the other groups.

Where this subdivision is demonstrable the groups are known as 'little' or 'micro-species'. Just as it may be shown by experiment that a species breeds true to the characters shared by all the micro-species of which it is composed, so, in like manner, it may be proved that members of a micro-species breed true to the characteristics which distinguish the group to which they belong. Nor does the

diversity which lies behind the crude disguise of specific uniformity end here. The individuals comprising a micro-species are not identical with one another. Some of them possess characters lacking or less pronounced in others, and of these characters some may be constant, reappearing in the offspring, and others may appear and disappear according to the conditions to which the individual is subjected. When it used to be taken for granted that a species is a fixed biological unit, any of its members which exhibit marked peculiarities were termed varieties, and in order to account for the existence of varieties it was assumed that there reside in living plants and animals powers which, whilst constraining them to produce their like, admit of small departures from identity of likeness—that is, of variation. Now, however, that it is evident that the term 'variety' covers several distinct kinds of difference, neither it nor 'variation' has a significance more definite than to connote the fact that forms of life, far from being immutable, possess capacity to change.

Just as a close view of existing species points to this conclusion, so also does a long view of the history of the world. When the procession of the living things which have appeared on the face of the earth, endured or disappeared, replaced by others, is reviewed, it suggests not changelessness but mutability. The fossil plants of the coal-measures are for the most part remains of green plants of kinds so different from existing trees and herbs that they cannot be classified with flowering plants nor regarded as their direct ancestors. It is, however, probable that when the carboniferous forests of strange vegetation flourished, flowering plants were already in existence, so high is their antiquity.

Nevertheless, although the exploration of the crust of the earth may show how remote is the origin of groups of plants now living, the succession of plants which it discovers suggests that life has not persisted from the beginning in a primitive, finished perfection, but has undergone progressive change. Some forms have evolved an increased elaborateness; others,

having reached this or that stage of complexity, have persisted unchanged for long geological epochs; and others again, once elaborate, have undergone simplification to such an extent that it may be difficult to say whether indeed they are primitively simple or are descended from more complex ancestors.

Study of the distribution of plants in space confirms the conclusion suggested by their distribution in time. Some species once widely distributed are now of narrow range. The maiden-hair tree (*Ginkgo biloba*)—as fossils testify—was long ago a native of this country and of large tracts of Europe. To-day this solitary representative of its genus is to be found nowhere in the world save in the gardens of Chinese temples, wherein priests have given sanctuary denied to it by Nature. The big tree of California (*Sequoia gigantea*) and the red-wood (*S. sempervirens*) are natives of narrow regions of western States of North America, and even there the red-wood exists only in a few restricted groves. Yet these great coniferous trees, now so solitary, were once of wider range.

At different periods, different hypotheses have been propounded to account for the evolution of plants and animals, but so far, although certain of them have found favour, none has met with universal acceptance. All the modern theories have this in common—that they take into account, as indeed must any evolutionary theory, the two apparently opposed facts of heredity and variation. The one, heredity, implies that parents transmit qualities to offspring; the other, variation, that offspring may exhibit qualities different from those of their parents. It follows, therefore, that the study of heredity and variation must be an essential preliminary to discussion of evolution. In this study the first question to be answered is: By what means is the passing on of qualities from parent to offspring contrived? The answer is to be found by investigating the processes of reproduction and by the experimental breeding of plants and animals.

As Chlamydomonas, that genus of apparently primitive, uni-

cellular green plants, served as an introduction to general plant physiology, so it may serve as a starting-point in the study of the physiology of reproduction. Species of Chlamydomonas perpetuate their kind in one of two ways. In certain circumstances the motile green cell (Fig. 3) which constitutes the individual, undergoing division and, it may be, redivision, gives rise to a group of two or more cells all seemingly alike, and like itself except that they are smaller. As Minerva sprang fully armed from the head of Jove, so these asexually produced, unicellular individuals (swarm-spores) spring by the

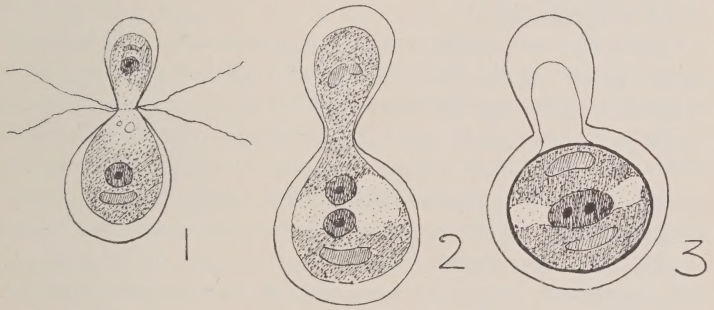


Fig. 41. Sexual reproduction of Chlamydomonas (sp.). (Adapted from Oltmanns.)

ultimate rupture of the mother-wall from the divided body of the parent-cell. They swarm out, go their several ways, and grow each into an adult individual in all respects resembling that which gave birth to them.

In other circumstances a new individual is produced by a totally different method. Two motile, green, Chlamydomonad cells (Fig. 41) approach one another, and, as happens in some species, slipping their coats, come in close contact. The nucleus of the one approaches that of the other and fuses with it, and the cytoplasms also become commingled, with the result that a single, new, unicellular individual is produced by the pairing of the nuclei and the mixing of the cytoplasms of two unicellular individuals.

Thus in Chlamydomonas and also in other unicellular plants two apparently distinct processes take place. The one, a sexual process, secures a reconstitution of the individual by the union of two individuals. The other, an asexual process, provides for the multiplication of the race. In higher plants and animals both results accrue from sexual reproduction. For in their multicellular bodies cells destined to fuse in pairs are produced often in vast numbers. They are the sexual cells or gametes, and when they fuse the product of each pair is a single-celled embryo, the zygote, from which in due course a new individual arises.

To pass at one stride from the reproduction of Chlamydomonas to that of the flowering plant is to miss so many facts of great evolutionary interest that there is every temptation to linger by the way in order to describe the reproductive processes of other kinds of plants—multicellular algae, liver-worts, mosses, ferns, and cone-bearing plants. Only by such study may the course of the evolution of the reproductive processes of plants be discovered. That, however, is a study in itself, and, though of the greatest importance to botanists and the professional student of evolution, is not essential to the present purpose, the investigation of the mechanism of heredity.

At first sight there would seem to be no manner of resemblance between the modes of reproduction of Chlamydomonas and the flowering plant. Yet the closer the scrutiny the more the methods of reproduction are seen to be identical.

The multicellular flowering plant, it is true, does not produce asexual, unicellular swarm-spores: nevertheless it retains large powers of propagating itself asexually by vegetative means, and by virtue of these powers not a few plants habitually multiply themselves. Many varieties of potato fail to flower, or if they flower, rarely set seed. The tubers serve for the propagation of the race. Daffodils planted in suitable soil increase a hundredfold in the course of a few years. The parent bulbs give rise each to numerous bulbs which, becoming detached, grow as independent plants, the flowers of which

in time take the winds of March with beauty. Brambles, besides reproducing themselves by seed, employ asexual methods for their increase. Their arching branches bend to the ground, and, where they touch it, the tips take root, and presently new plants, casting themselves adrift from the old, arise from the buds of each self-planted branch. The elms of England owe their commonness and alignment in hedgerows to the power which the trees possess of giving rise to suckers from their roots, and countless other wild and cultivated plants use vegetative means of propagation. Some, indeed, may have no other way of propagating their kind. The American water-weed (*Elodea canadensis*), which chokes the Cam and abounds in many other rivers, propagates itself in this country solely by separation of the plant into fragments; for only the female of this plant has established itself here.

Most flowering plants, however, reproduce their kind by means of seeds, the embryos of which arise as a result of sexual reproduction. Any one who surveys the marvellous variety of form and elaborateness of construction met with among flowers may well imagine that the process of sexual reproduction in flowering plants must be far more complex than is that of Chlamydomonas. Yet it is not: the preliminaries are more elaborate, but the act of fertilization is as simple in the flowering plant as it is in the unicellular green alga.

Much of the complexity of construction which flowers display has reference not directly to reproduction but to pollination—that is, the deposition of pollen shed by the anthers of a flower on the only part of that flower or of another of the same species on which pollen grains may grow, and so play their part in fertilization. Thus it is that flowering plants exhibit remarkable series of floral mechanisms, from relatively simple types such as those of buttercups, to highly elaborate types such as those of daisies; series which culminate in the most intricate complexity, e. g. in Orchids (Fig. 42), many of

which are described in fascinating manner in Darwin's books on *Forms of Flowers* and *Orchids*.

The flower of a flowering plant consists of several sets of members, each of which may be readily recognized in a flower of simple construction such for example as magnolia (see Fig. 43). Outermost is the perianth, consisting in the magnolia and some other flowers of a set of uniform members, but often showing differentiation into calyx and corolla. In the latter case the calyx is composed either of separate leaf-like sepals, or of sepals united with one another. They serve to protect the more delicate members of the flower-bud which they enfold. Within the calyx, and also either free or joined together, are the petals, which are known collectively as the corolla. Petals are often of brilliant colour, and from them often odours emanate—sometimes pleasant and attractive alike to human beings and to bees and other insects, and sometimes unpleasant to our senses, yet seductive to flies which may serve as pollinating agents of such carrion-smelling flowers. The joined petals in primulas and many other plants form a tube which contains nectar, a sugary liquor attractive to bees, moths, and other insects. Colour, odour, nectar, all contribute to the alluring of insects to the flower. Length of the corolla tube and general construction of the flower serve, whilst facilitating the effective visits of some given kind of insect, to discourage other kinds—for example, those with shorter proboscides—from sucking the nectar beyond their reach. The construction, moreover, is such that when the right kind of insect visits the flower in search of nectar or pollen, some part of its body brushes against the stigma and later against the stamens. If the latter are ripe, as the insect flies away pollen is deposited on its body and is transferred to the stigma of another flower : and so flying from flower to flower of a species the insect pollinates each in turn.

By these means, the details of which are as varied as they are beautiful, many species are cross-pollinated. Although in a large number of species cross-pollination is the rule, there

FIG. 42. Flower of *Cypripedium Leeanum*. Cf. Fig. 43.

are many in which self-pollination occurs. In the common pea (*Pisum sativum*), for example, although the lines on which the flower is built indicate that it was once effective in securing cross-pollination, the flowers are now habitually self-pollinated. When the bud is about to open, the stamens, the anthers of which are arranged ringwise around the stigma, shed their pollen directly on the stigma. Yet other papilionaceous flowers—the gorse, for instance—possess a not dissimilar mechanism which has remained highly efficient in securing cross-pollination by bees. On an early summer morning, when the air is heavy with the honey scent of gorse, the insects pass incessantly from flower to flower intent on gathering honey, and casually, but surely, transferring pollen from one flower to the stigma of another.

In spite of its importance in pollination, the corolla, like the calyx, consists not of essential members, but of members accessory to fertilization. A plant may be caused to set seed after calyx and corolla have been artificially removed.

The essential members of the flower are the stamens and the pistil. The stamens may be known by the fact that, when ripe, they—or rather, the anthers, which are their chief part—burst and discharge, sometimes gently, sometimes explosively, the pollen which is formed in them in the course of their development. More centrally placed than the stamens is the pistil. In some flowers and those the simpler ones—as, for example, the buttercup and magnolia (Fig. 43)—there are numerous separate pistils: in others (Fig. 44 A) only one. The pistil becomes in course of time the seed-vessel. It consists of three parts; a lowermost, swollen, bag-like ovary, which contains one or more minute, whitish ovules. Each ovule consists of a shortly-stalked, more or less spherical mass of tissue which, when fertilization takes place, grows and develops as the seed. Above the ovary, the pistil is continued as a longer or shorter column of green tissue—the style, which ends in a knobbed, plate-like or lobed stigma, recognizable in the case of many flowers either by its hairiness or

stickiness when ripe. In flowers which are dependent on the wind for pollination, maize and other grasses, &c., the stigmatic surfaces are large and more or less feathered owing to the outgrowth of long hairs, so that with wide expanse of surface the chances of wind-borne pollen reaching the stigma are much greater than they would be were the stigmatic

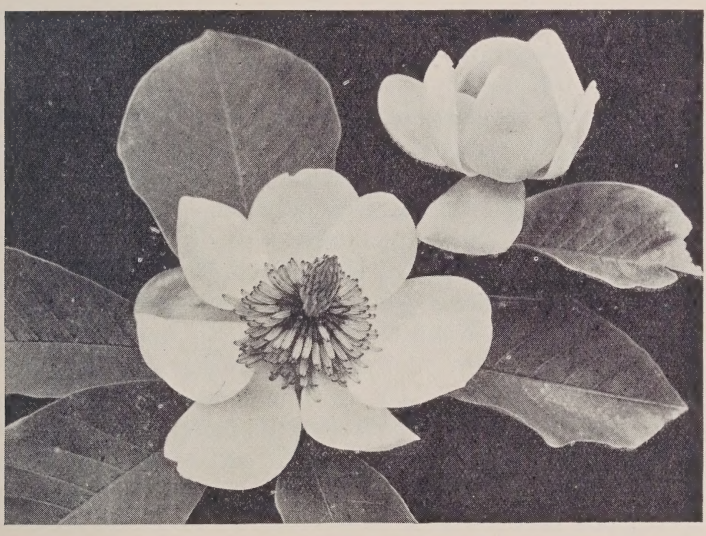


FIG. 43. *Magnolia Watsoni*, showing simple type of floral construction with numerous stamens and carpels. Photograph by Malby.

surface small, as it generally is in species which are pollinated by the more precise agency of insects.

That stamens and pistil are essential for reproduction may be demonstrated by experiment. If some easily manipulated flower be emasculated—that is, the stamens removed from it whilst in the bud stage and before they have burst—provided that chance pollen of the species is prevented from reaching the stigma by covering the flower with a thin paper-bag, no seed is set. If, however, pollen of that or another

flower of the same species be dusted on the ripe stigma, seed is set in due course.

The processes which go on between pollination and fertilization may be followed by microscopic observation. That pollen grains are capable of an independent, albeit ephemeral, existence may be shown by planting them in sugar solution. Provided the pollen be ripe, and the solution of the right strength, the grains absorb water and swell and their living contents undergo division. Although, when first formed, the young pollen-grain consists of a single cell, by the time it is ripe it is composed of two. One of these cells has for its function the formation of a pollen-tube. It grows and pushes out its wall in the form of a tube, which emerges through one of the thin places usually found in the otherwise thick and symmetrically-sculptured wall of the grain. The pollen-tube, which becomes of considerable length, may be seen under the microscope to contain cytoplasm and two nuclei, which have arisen by the division of the other of the two cells of which the adult, ungerminated pollen-grain consists. Germination in all respects similar to that which occurs in the sugar solution takes place in the flower, provided that the pollen grains fall on the stigmatic surface, and that they are from a flower of the same species. If pollen from another species falls on the stigma, as in Nature it often does, it generally fails to germinate. In comparatively rare instances the 'foreign pollen' may grow and fertilization may ensue, with the result that a hybrid is produced. In this manner, both in Nature and under cultivation, numerous hybrids have arisen between species, and particularly among Orchids—a family which stands apart from others in the facility with which not only different species of a genus, but even plants belonging to different genera, hybridize with one another.

During the time that the stamens are forming and ripening pollen, the ovules undergo development. An ovule arises from the ovary as a little hummock of tissue consisting of cells derived from the epidermal and sub-epidermal layers. At

first, each ovule consists of a naked mass of more or less similar cells, but presently it becomes enclosed in one or two coats (integuments) which form the seed-coats (Fig. 44). The integuments grow up around the ovule, completely investing it save at the apex, where, ceasing to grow, they leave a narrow open way, the micropyle, which gives access to the ovule. Though difficult to see in the ovule, the micropyle is

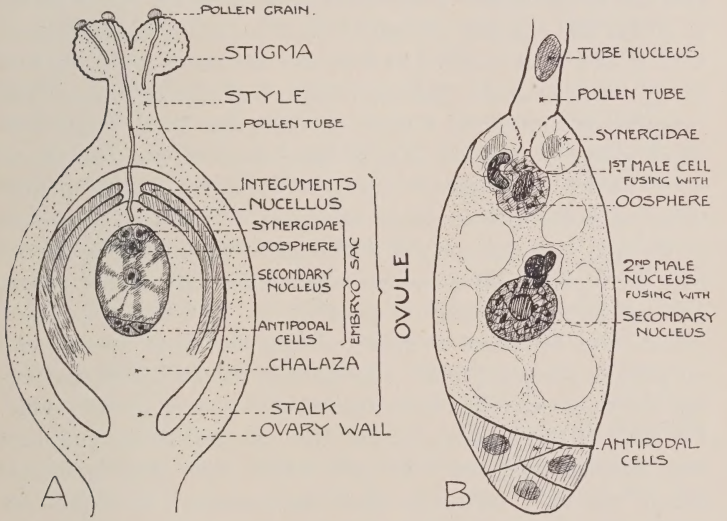


FIG. 44 A and B. Diagrams illustrating (A) the structure of the pistil and (B) the process of fertilization (see text).

often evident in the seed-stage, in which it appears as a minute hole, beneath which lies the tip of the root of the embryo. Complex changes go on in the developing ovule. The changes are, indeed, so curious as to make it certain that they have behind them the compelling force of a long and varied evolutionary history; but since these changes in the developing ovule would only be significant if that history were traced, and inasmuch as that is a long story, only the essential parts of an ovule ready for fertilization will be described.

Lying beneath the surface of the ripe ovule, just below the micropyle, is a large nucleated cell—the oosphere or female gamete. It is accompanied by two other cells (the synergidae) which disappear during fertilization, and in all probability aid the process, without, however, taking a permanent part in it. Lying in a vacuolated, central mass of cytoplasm are other nuclei (see Fig. 44 A and B). Of these, two are of interest. They come, one from an upper group of which the egg-cell (oosphere) and the two cells associated with it are a part, and one from an antipodal group of four nuclei formed at the opposite, basal end of the ovule. The two nuclei, sometimes known as the polar nuclei, approach one another, and either fuse at once to form one (the secondary nucleus) or await events. Meanwhile, the pollen-tubes of pollen-grains deposited on the stigma have grown, as foreign, parasitic plants might grow, through the central part of the style, and have reached the cavity of the ovary. Arrived there, instead of growing in any direction, each pollen-tube, attracted no doubt chemically, finds its way to a micropyle, pushes through that narrow channel, and, flattening out at its end, lies close against the surface of the ovule. The wall at the flattened end of the pollen-tube becomes soft and mucilaginous, and the two nuclei (the male gametes) which the tube contains, each accompanied no doubt by some—albeit very little—cytoplasm, are ejected through the liquefied wall and enter the ovule. One of the male gametes approaches the egg-cell, its nucleus penetrates the cytoplasm, and reaching the female nucleus lies for a while beside it. Ultimately the male and female nuclei fuse with one another, so that one nucleus is formed. Any cytoplasm which accompanied the male nucleus and entered with it into the egg-cell fuses with the cytoplasm of the latter. Thus by nuclear and cytoplasmic fusion the fertilized egg-cell or zygote is formed. A new individual has been brought into being.

A cell-wall is organized about the fertilized egg-cell. After a longer or shorter period of rest, the zygote begins to divide, and before the ovary-wall ripens to form the fruit the zygote

has built itself into a miniature, multicellular plant, with a small root lying close to the micropyle through which it is destined to emerge when germination begins, a stem terminating in a bud and one or two of seed-leaves (Fig. 11, p. 39). Thus it is manifest that the process of fertilization of the flowering plant is in essentials identical with that of Chlamydomonas. In the one, as in the other, two gametes meet, and give rise to a single cell, the zygote, which is the beginning of a new individual. In Chlamydomonas the individual is unicellular, and so the zygote has nothing to do but grow. In the flowering plant the unicellular zygote must needs undergo division and redivision before the adult, multicellular individual is formed, and the cells to which it gives rise must also undergo differentiation until they appear as units of one or other of the members—root, stem, or leaf—of which the young embryonic plant is composed.

The fate of the two nuclei which were left awaiting events deserves recording. As they approach, or sometimes after they have met, a third nucleus appears near them. It is the second nucleus of the pollen-tube—the second male gamete. That nucleus is in any case debarred from fusing with the female gamete, for, so soon as the one male gamete has effected fertilization, chemical change occurs in the zygote which prevents the entrance of another. Passing by the egg-cell, the second male gamete meets the two nuclei. They all fuse together to form one microscopically and physiologically monstrous nucleus. The nucleus formed by the triple fusion is termed the endosperm nucleus. By its division, and the subsequent division of the cytoplasm surrounding it, the nucleus gives rise to the endosperm (see p. 36), the tissues of which become filled with starch or oil and protein food-materials derived from the mother-plant. From the endosperm the developing embryo draws supplies of nourishment. Thus there is, as it were, in the flowering plant a double fertilization; one, the true fertilization, as a result of which the zygote, and subsequently the embryo, are formed; the other an accessory fertilization, having

nothing directly to do with the formation of the new individual beyond providing a mass of food-material on which that individual may draw in its young stages before it has become large enough to push its way out of the seed, establish itself in the earth, and fend for itself.

Pollination and fertilization evoke secondary changes in the flower. So soon as pollen is deposited on the stigma and its germination begins, changes of growth and development occur in the ovary walls and, it may be, in other parts of the flower. The ovary walls become the fruit walls, and as the seeds mature, the fruits, undergoing change of one kind or another, enlarge and ripen also. The ovary walls may become fleshy or so woody that only by their decay is the seed liberated; or, becoming membranous, the walls may finally burst, separating into sections along lines of weakness so that the seed is liberated, falling out gently, as in the violet, or flung out suddenly, as in the gorse.

All manner of mechanism facilitating the liberation and dispersal of seeds is to be found among plants; minute seeds which float in the air, winged seeds, burred or winged fruits, fruits with parachute mechanism as in the dandelion, fleshy fruits attractive to birds with seeds which resist digestion, fruits like those of the coco-nut, which float and germinate after long immersion in salt water so that, as men are used to say, the coco-nut only grows by the sea or within the sound of the human voice. All these, and countless other mechanisms, serve—with what efficiency the ubiquity of vegetation shows—to ensure the sowing of plants in their special plots over the surface of the earth.

The facts concerning the process of sexual reproduction which have just been related bear on the nature of heredity in plants and animals. Each parent makes a material contribution to the body of the offspring; which body is indeed composed of the nuclear and cytoplasmic material contained in the male and female gametes by the fusion of which the new individual is produced. It is possible to draw a

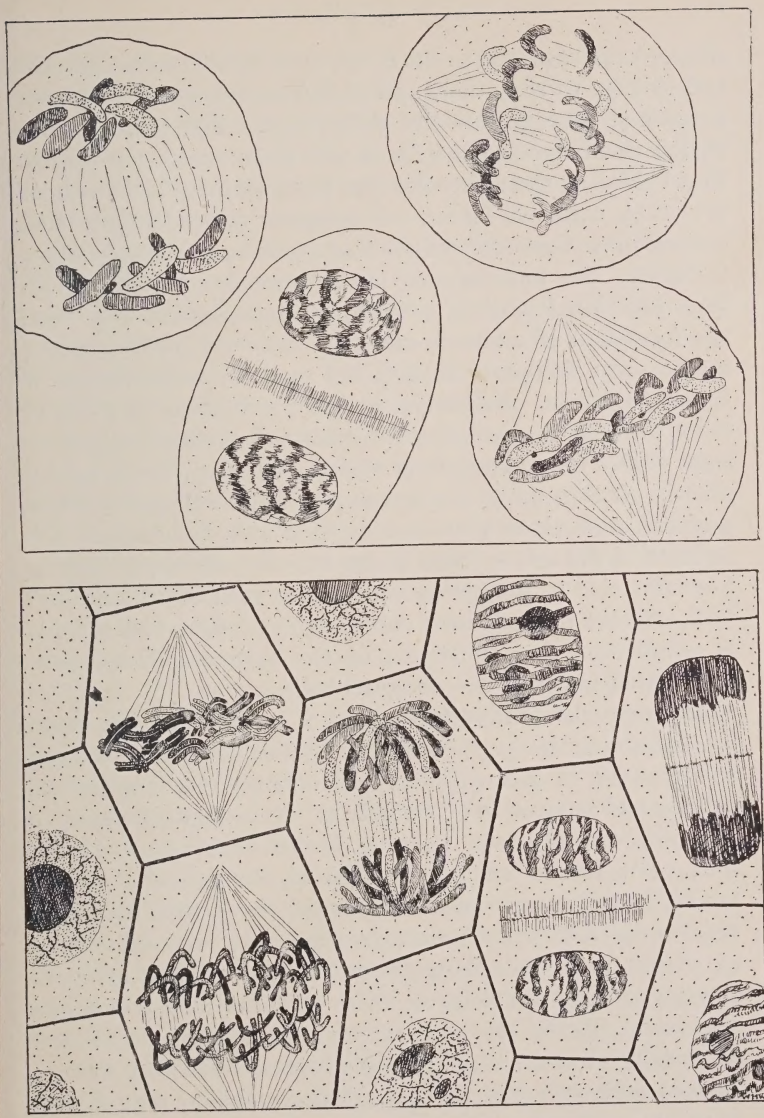
further conclusion from the facts of sexual reproduction. In the description of the process as it occurs in the flowering plant it was pointed out that the male gamete, though surrounded by cytoplasm whilst in the pollen-tube, at the time of its approach to and fusion with the female cell, consists entirely, or almost entirely, of nuclear material. This is true also of many other kinds of organism, plant and animal. In them, though the egg-cell (female gamete) contains cytoplasm as well as nucleus, the male cell, which is often far smaller than the female, is composed mainly or exclusively of nuclear material.

Inasmuch as the facts of life and the experimental investigation of heredity indicate that male parents have on the average no less influence on the form and qualities of offspring than have female parents, it follows that the material basis of heredity must reside in the nuclei of the gametes. This, be it noted, is by no means to say that the cytoplasm of the egg-cell is without importance. It manifestly provides, with or without any contribution from the male gamete, the cytoplasm of the zygote. In the case of green plants it contains also one or more leucoplasts, by the subsequent division of which all the leucoplasts and chloroplasts of the body are begotten. Nevertheless, so far as heredity is concerned, it is the nucleus—that of the male and that of the female gamete—that is of paramount importance. This conclusion becomes the more certain the more the structure and behaviour of the nucleus are investigated, and the more the course of inheritance of plant or animal characters is studied.

Reference has been made repeatedly to the process of cell-division in the plant, but the details of the process have been reserved for consideration in this place. When an ordinary vegetative cell, as, for example, a cell of the growing-point of a stem or root, is about to undergo division, significant changes occur in the nucleus (Fig. 46). During the intervals between divisions, the nucleus of the resting or growing cell presents a fairly homogeneous appearance. Parts of it, however,

stain more deeply than others, so that the nucleus under the microscope may exhibit a somewhat granular appearance. The nucleus of a cell about to divide heralds the fact by a series of elaborate changes. The net result of these changes (cf. stages in Fig. 46) is the appearance of a coiled thread beset with deeply staining masses of material, as a necklace may be threaded with coloured beads. The thread becomes less and less closely coiled and presently takes the form of a series of distinctly separate lengths. These are the chromosomes. They are living members of the cell, possessing, like the cell itself, powers of assimilation, growth, and division. The number of chromosomes which appears in the course of nuclear division of any vegetative cell of a given species of plant may be so few as five, or so many as thirty-six or more ; but whether large or small it is constant. The number in Fig. 46 is sixteen. Not infrequently differences of shape and size are exhibited by the chromosomes of the dividing nucleus, and when they occur the differences are likewise constant, reappearing in each successive division of the species in question.

The regular recurrence of chromosomes of distinctive form and constant number suggests strongly that the chromosomes possess each an individuality of its own. Speaking generally, the chromosomes—which are, of course, of microscopic size—are rod-, V-, or somewhat comma-shaped, or more or less spherical. At first they lie irregularly and confused with one another within the vanishing outlines of the nucleus, but at a later stage the chromosomes separate from one another and congregate in the central or equatorial region of the cell, where they range themselves more or less symmetrically in one plane (Fig. 46). When or before the equatorial-plate stage is reached each chromosome appears no longer as a single but as a double thread, looking as though made up of two longitudinal halves. In the meantime fine protoplasmic fibrillae—the spindle-fibres—with staining properties very different from those of the chromo-



FIGS. 45 and 46. Semi-diagrammatic representation of nuclear division. Mitosis (below) and meiosis (above) in *Allium* sp. (Adapted from Tischler.)

somes, have appeared in the cell. They stretch from near one end or pole to the other, and at either end merge in denser masses of protoplasm—the polar caps. The chromosomes attach themselves to the fibres and their separation begins. The halves of each chromosome part company. Drawn or driven by unknown forces, one daughter contingent—that is, one set of half-chromosomes—reaches one pole and the other the other. The journey over, the chromosomes become coiled, their individual outlines cease to be recognizable, and, with the formation of a membrane, each daughter nucleus passes into a state similar to that of the mother nucleus before it began to divide. Following on nuclear division, a plate of clear protoplasm becomes differentiated across the cell at right angles to, and generally midway between, the daughter nuclei. Within the protoplasmic plate, cell-wall substance is secreted, and ultimately may be seen stretching across the equator of the cell to form a new cell-wall, which, extending from one side to the other, and joining with the mother-cell wall, divides the cell into two daughter-cells. Cell-division is complete. The substance of the mother-cell has been distributed between two daughter-cells.

Any one who follows the course of nuclear division, stage by stage, must be impressed both by the constancy of form and number of the chromosomes, and by the longitudinal halving and separation of the halves. If, as there is reason to suppose, chromosomes have a necklace-like construction, that of a thread on which different things—priceless, so far as the cell is concerned—are strung along, then the longitudinal division of each chromosome would serve admirably to ensure that each daughter-cell should receive identical dowries of all the articles of value that the mother nucleus possessed. Should this happen, then the daughter nuclei are, potentially at least, in all respects identical with the mother nucleus and with one another. Differentiation may subsequently lead the daughter-cells along different paths to very different destinies of form and function; but the daughter-

cells are born equal—so far, at all events, as the chromosome-constituents are concerned. It is therefore permissible to conclude that daughter-cells produced by the process of cell-division just described inherit the qualities of the mother-cell because they are made each of equal halves of the essential living substance of that cell.

Observation provides confirmation of these conjectures. Plants propagated vegetatively by cuttings, &c., reproduce (with certain exceptions not easy of interpretation) not only the general but also the peculiar characteristics of the parent. It is indeed a regular horticultural practice to employ methods of vegetative propagation in order to maintain and multiply rapidly varieties of fruit trees, roses, and other garden plants which may not, and in many cases do not, breed true from seed. Inasmuch as plants propagated in this way are but detached parts of the parent plant, it is not perhaps surprising that they should prove to be identical with the plant from which they are taken.

In sexual reproduction, on the other hand, two cells, the male and female gamete, fuse to form the new individual. If therefore the gametes possess each the number of chromosomes characteristic of the nucleus of a vegetative cell, the gametes in fusing would each contribute that number, and hence the zygote would have twice the number, and so on for each generation—which is absurd. In point of fact there comes a moment in the development of the individual when the plant, having completed the growth of its body, proceeds to the elaboration of those tissues contained in the anthers and ovules from which the sexual cells are to arise. When that moment arrives the nuclei of the cells concerned no longer divide mitotically—that is, after the fashion already described. The differences between the behaviour of the dividing nucleus in body-building cell-divisions and in meiosis (that is, the division which marks the beginning of the formation of gamete-producing tissues) are illustrated in Figs. 45 and 46 and again in diagrammatic form in Fig. 47, which represents

the two types of nuclear division in the case of a species the vegetative cells of which have each six chromosomes.

As Fig. 47 indicates, in the division which ushers in the formation of gamete-producing tissues, the chromosomes when they range themselves about the equatorial region appear to be of half the somatic number—in the case chosen, not six, but three. The appearance of the half number is, however, as deceptive as appearances are apt to be. The three are six; for each of the three consists of two chromosomes paired with one another. Lying in close contact all along their length the two paired chromosomes look like one. The two members of each pair do not divide longitudinally as in preceding mitotic divisions, but when the spindle-fibres are formed the paired chromosomes separate. One whole chromosome of a pair goes to one pole and the other to the other, and thus the nucleus of each daughter-cell contains three and not six chromosomes. On this account the division is often referred to as the reduction division. In it the number of chromosomes which characterize the mitotic cell-divisions, whatever that number may be, is halved, and hence it is convenient to refer to this number as the haploid and to the double number characteristic of mitosis as the diploid. The subsequent divisions of the daughter-cells produced by reduction division follow in the main the diploid type. In them the chromosomes meet at the equator and each splits longitudinally, so that the daughter-cells have each the reduced number of chromosomes. Presently the male and female sexual cells are organized, and they also have the haploid number. Hence, when fertilization takes place and the gametes fuse, each contributes its contingent, and so in the zygote the original diploid number of chromosomes is restored. In general terms, the zygote and the diploid phase possess $2n$, the haploid phase and the gametes n chromosomes.

When, however, the histories of the paternal chromosomes, that is, those contributed by the male gamete, and of the maternal chromosomes, those contributed by the female

gamete, are traced, it is discovered that whereas all remain distinct and divide longitudinally during the mitotic divisions

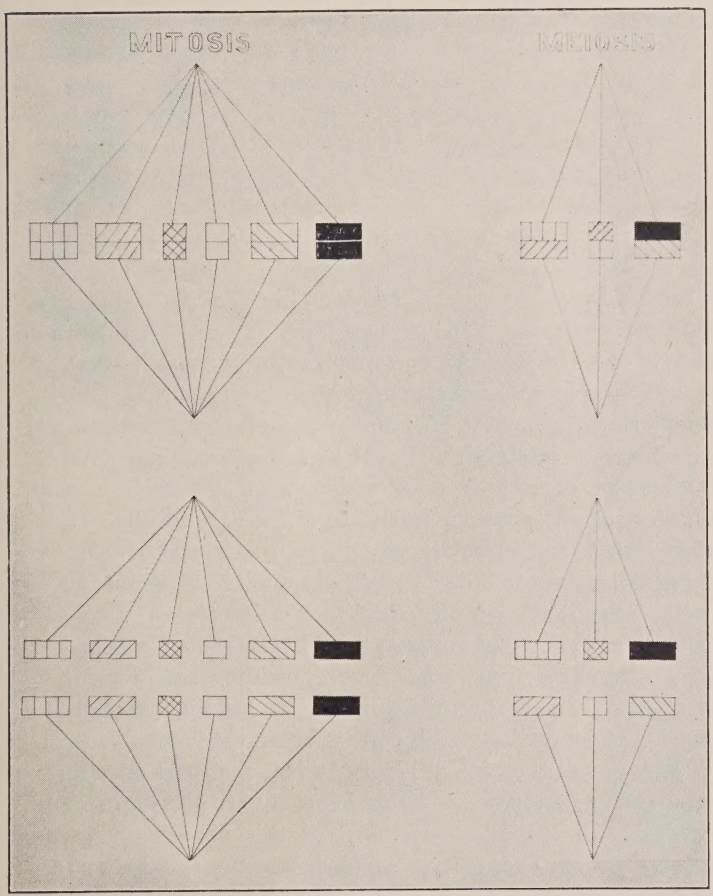


FIG. 47. Diagram of mitosis and meiosis (see text).

in the course of which the body of the new individual is organized, at the reduction division the male and female chromosomes pair with one another, each paternal chromo-

some mating with a corresponding maternal chromosome. Throughout all the divisions of the diploid phase the $2n$ chromosomes take up positions side by side on the equatorial plate, and each divides longitudinally, so that every cell has a complete equipment of paternal and maternal chromosomes ; but in the reduction division paternal pairs with maternal chromosome, and when each paired chromosome separates into its maternal and paternal constituent one of each pair—either that chromosome originally brought in by the male gamete or that brought in by the female gamete—goes to one daughter-cell and the other to the other daughter-cell. Hence, with respect to each of its chromosomes, a nucleus produced by the reduction division is derived either from the paternal or the maternal side. The nucleus of a body-cell, on the other hand, is of both paternal and maternal provenance—that is, has all the chromosomes contributed by the male gamete and all contributed by the female gamete. Gamete stands to body-cell as a simplex stands to a duplex thing. Which chromosome of a pair goes which way—to this or that daughter-cell—is apparently left to chance to decide. If so, and inasmuch as the number of gametes produced by a plant is very great, chance will decree that all possible distributions of chromosomes shall occur in equal proportions in the gametes.

The behaviour of the chromosomes in the reduction division—pairing and meeting in the zygote, residing side by side in the cells of the body, dividing longitudinally, growing to maturity and dividing again continuously throughout successive divisions of the diploid phase, to pair and part once more in the reduction division—provides a clue to the nature and mechanism of heredity. In view of this behaviour it can scarcely be doubted but that the chromosomes are the bearers of definite, material things, each of which has a definite place in one or other of them. These things, numerous and distinct, are to be regarded as operating each in the cells of the plant to give rise by their several and co-ordinated activities to the characters which are collectively the expression of the individ-

uality of an organism. These material things, borne each in its place in a given chromosome, like objects in a meticulously ordered chest of drawers, may be termed factors, and it may be assumed with confidence that each factor has a special work to do in giving expression to the life of the cell and to its peculiarities of form and behaviour. Inasmuch as the body is the expression of the activity and peculiarities of the cells which constitute it, the factors strung along the chromosomes are eventually responsible for the form and peculiarities of the individual.

It becomes, therefore, of the greatest interest to inquire whether the known facts of heredity fit in with those based on microscopic investigation of the dividing nucleus. The inquiry must of necessity take the form of a review of the knowledge of heredity gained by the scientific breeding of plants and animals. This subject, the experimental investigation, by breeding and other means, of the mode of inheritance of the characters which distinguish each kind of plant and animal is termed Genetics.

Since man began to think at all, the problems of genetics have intrigued and vexed him. The problems seemed, however, so intricate that, though a vast number of facts was gradually accumulated, and although hints of order were everywhere apparent, little progress in discovering the laws which determine the order was made until a man of genius, Gregor Mendel, set himself to work upon the task. He was the Abbot of Brunn in Austria, and made his experiments in the monastery garden.

The reasoning which led Mendel to experimentation must have been of this kind: Men, in their attempts to discover the laws of heredity, have been thwarted by the complexity of living organisms. I will ignore the complexity. I will take the organism to pieces, and examine the course of inheritance of each piece. I will investigate the mode of inheritance of one bodily character at a time. We grow in this garden different races of peas. Some have seeds with yellow skins

and some with green skins. Some races have round seeds and others that we like better—marrow-fat peas—have wrinkled seeds. Some races grow so tall as to need stakes to support them, others are dwarf and need none. Ordinary people may scoff and say that these are trivial characters, but I have Divine authority to think otherwise—for was it not said, ' the hairs of your head are all numbered ? ' and what forsooth is trivial and what is important in life, who shall say ? And so Mendel set to work. He mated the yellow- and green-seeded races of peas, the round and wrinkled and the tall and dwarf, and found order in inheritance everywhere.

Following Mendel's initiative, others have made similar breeding experiments, and have confirmed and extended his results. During the past twenty years a great variety of plant- and animal-characters has been subjected to breeding tests : leaf-shape, flower-colour, resistance and susceptibility to disease, annualness and perennialness, earliness and lateness of flowering, doubleness and singleness of flowers, variegation, baking qualities of flour, hardiness and tenderness, stature, fertility, sterility, and so on.

Although it cannot be stated that it has been possible to subject all kinds of plant-characters to the test, yet it may certainly be claimed that the inheritance of characters of a great number of kinds, trivial and important, morphological and physiological, have been investigated fruitfully by the method. An example, not taken from Mendel's work but from that of some of his English disciples (Bateson and his colleagues), will suffice to illustrate the general conclusions reached by Mendel.

The Chinese primula (*Primula sinensis*) is a very variable plant. Some varieties have ' palm ' leaves—that is, leaves of palmate shape ; others have ' fern ' leaves—that is, of a more pinnate shape (Fig. 48). Varieties exist which breed true to the palm-leaf character. Self-fertilized or crossed with one another, all the offspring which they yield have palm-leaves. Other varieties breed true to fern-leaf character.

If one of the true breeding, palm-leaf plants be crossed with one of the fern-leaf plants, the offspring of the cross, known as the first filial generation (F_1), are all palm-leaf. Thus :

Palm × Fern
|
F_1 . . . . . Palm

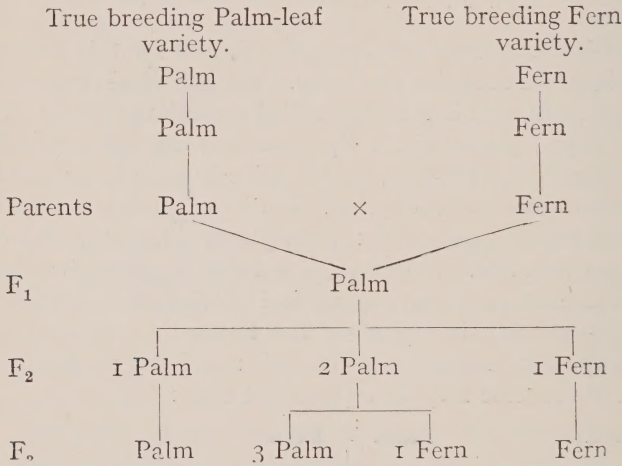
The fern-leaf character has disappeared, and for this reason it is known as a recessive character. The palm-leaf character manifests itself, and is therefore called a dominant character.

If, however, plants of the F_1 generation are self-fertilized or crossed with one another, the recessive (fern-leaf) character reappears in some of the offspring. The second or F_2 generation presents a mixed appearance : some plants are palm-leaf and others are fern-leaf. Moreover, if a large F_2 generation be raised it is discovered that a numerical relation exists between the palm- and fern-leaf plants. The larger the number the closer is the approximation to the ratio :—3 Palm : 1 Fern. So that the scheme may be represented thus :

Parents	Palm	×	Fern
F_1	Palm		
F_2	Palm	:	Fern
	3	:	1

Orderliness of genetical behaviour is observed also in subsequent generations. If fern-leaf F_2 plants are self-pollinated they give rise, generation after generation, to nothing but fern-leaf plants. They breed true to that character. If, on the other hand, F_2 palm-leaf plants are self-fertilized, although the plants used in the experiment look alike with respect to leaf-shape, the kinds of offspring they produce show that they are not alike in constitution. Thus, if a large number of palm-leaf F_2 plants be self-fertilized and

the progeny of each kept separate, it is found that on the average one in every three breeds true to that character, and that the other two behave in a manner similar to the palm-leaf F_1 plants: they give rise to offspring of which three are palm-leaf and one is fern-leaf. Thus the full genetical scheme may be represented:



Three facts of manifest importance emerge from the experiment.

The first is that the inheritance of a given character is orderly: it follows a definite course.

The second fact is that plants, e. g. palm-leaf *Primula sinensis*, may look to be identical, and yet may be shown by their offspring to be of different constitution. For example, one of every three F_2 palm-leaf plants breeds true, the other two do not.

The third fact, which clearly has some relation with the foregoing, is that a character—such, for example, as fern-leaf which fails to appear in the F_1 offspring—may reappear, or, as it is said, segregate out in the following, F_2 generation. Thus, in the F_2 generation, fern-leaf segregates from palm-leaf, so that some of the offspring are fern-leaf and some palm.

Appeal to the facts of sexual reproduction and to the

behaviour of the chromosomes in the reduction division helps to make these genetical rules intelligible.

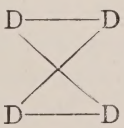
The hypothesis of factors suggested in the course of the study of nuclear division may be applied to the elucidation of the behaviour of the several generations resulting from the crossing of palm- and fern-leaf plants. It may be assumed that a factor exists which when present causes a leaf which, in its absence, would be of the fern type to develop the ' palm '-shape. It may be denoted by some conventional sign, as, for example, a capital letter. Let D stand for the factor for palm-leaf. In like manner let d stand for absence of the factor. True breeding palm-leaf varieties give rise, whether selfed, or crossed with one another, only to palm-leaved plants. How this comes about is shown by the scheme :

Pure Breeding Palm-Leaf Plant

D D

yields gametes D, D, that is, of one kind only.

male gamete × female gamete



yields zygotes all D D

i.e. all Palm-leaf.

When, however, a race pure to the character is crossed with one pure to the recessive fern-leaf character, the scheme is as shown in Fig. 48, p. 217. Of any four F_2 plants, three have the dominant factor D = palm-leaf, and of the three, one = (DD) is pure bred (homozygous) for the factor, and hence produces in subsequent generations only palm-leaf plants. The other two of the three are (Dd), i. e. not pure bred but heterozygous for the palm-leaf factor. They give rise when self-fertilized to both palm- and fern-leaf plants in the ratio of 3 : 1. The remaining one of the four

is (dd), that is, it lacks the factor for palm-leaf, is therefore fern-leaf, and breeds true to that character.

Any one who will look at the scheme from the point of view of the behaviour of chromosomes in meiosis will recognize that the genetical and cytological facts supplement one another in precise and elegant fashion. Suppose that the factor D occupies a definite place in one of the chromosomes. In the pure-bred palm-leaf plant, D is contributed by both male and female gametes. The zygote and each body-cell have, therefore, the factor D in one paternal and one maternal chromosome. At the reduction division these chromosomes separate, but whether the male or the female chromosome goes to a gamete, that gamete carries the D factor. On the other hand, in the cross palm × fern, male and female gametes of the palm-leaf parent each carry factor D, and male and female gametes from the fern-leaf parent each carry the recessive factor d. Therefore, in the cross, one parent brings in D and the other d. The zygote is Dd and the body-cells are Dd, that is, of the chromosomes which provide a domicile for the factor, one carries D and the other carries d. At the reduction division the D chromosome and the d chromosome pair and part, and therefore when the gametes are formed, half of them will contain D and half d. This being true for both male and female gametes, their chance mating must give on the average :

1 DD, 2 Dd, 1 dd

		Male gametes D	Male gametes d
Female gametes	D.	DD	Dd
	d.	Dd	dd

Many other examples of this kind of Mendelian inheritance have been discovered. It need scarcely be said, however, that by no means all characters show such a simple genetical

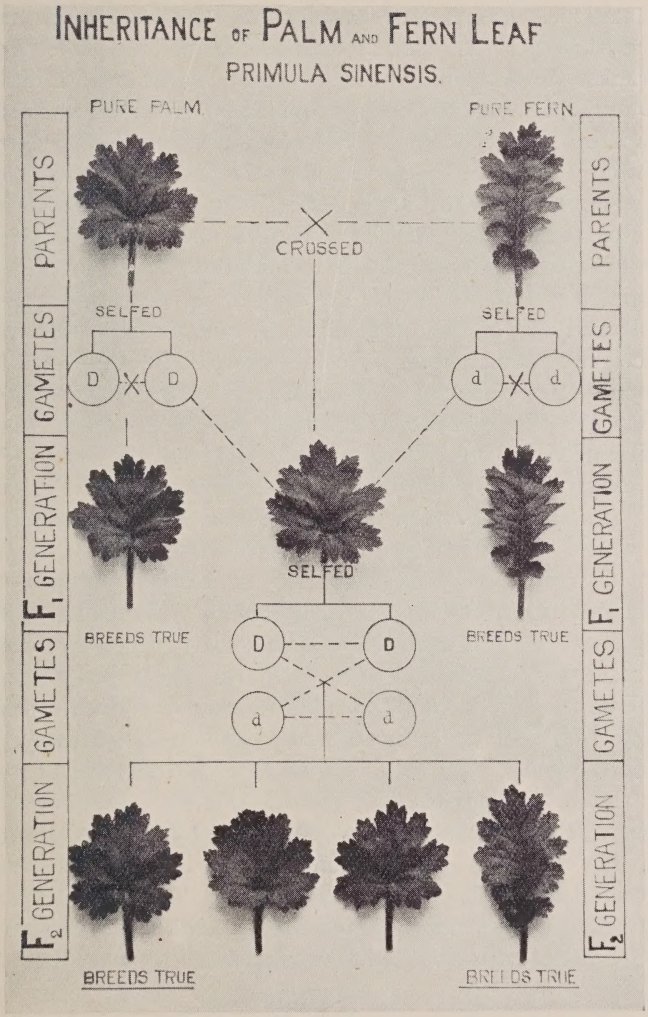

INHERITANCE OF PALM AND FERN LEAF
PRIMULA SINENSIS.
PURE PALM
PURE FERN
PARENTS
CROSSED
SELFED
SELFED
GAMETES
D
D
d
d
F1 GENERATION
BREEDS TRUE
SELFED
BREEDS TRUE
F1 GENERATION
GAMETES
D
D
d
d
F2 GENERATION
BREEDS TRUE
BREEDS TRUE
F2 GENERATION

FIG. 48.

behaviour. Life is very complicated, and heredity, as everybody knows, often follows strange courses and plays curious pranks. Some of the apparent complications are not difficult to unravel. Dominance is, as might be expected, not always apparent. For example, the cross between red and white flowers of certain species results in a pink F_1. When, as in the pure red race, each gamete carries a colour-forming factor, the zygote receives two factors, one from either parent, and the two are so strong as to make the flower produce red pigment; but when the cross between a member of the coloured and of the white-flowered race is made the zygote receives only one factor for colour production, and that factor is only strong enough to make flowers pink.

In the case of other characters, two or even more factors must needs be present to produce a given character. This is exemplified by the colour of certain flowers, e. g. sweet pea (*Lathyrus odoratus*). If either factor be absent the flower is white. The sweet pea as it grows wild in Sicily has, and breeds true to, purple flowers. In Nature perhaps, and certainly under cultivation, many colour varieties—red, blue, salmon, rose, and white have arisen. If two factors must be present for any colour to arise in the sweet pea flower, it follows that there should, or might, occur two kinds of white-flowered sweet peas, looking identical as to whiteness but differing genetically from one another, in that one lacks one of the two colour-forming factors and the other lacks the other. Representing the colour-factors by the letters C and R, the factorial composition of one homozygous white-flowered race will be CCrr, and that of the other ccRR, and the result of the cross between the two will be the production of F_1 plants with coloured flowers. Thus:

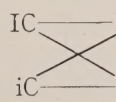
Parents:	White	×	White
	CCrr	×	ccRR
Gametes:	Cr	×	cR
F_1	CcRr		
	Coloured		

This genetical sleight of hand was actually performed during experiments made some years ago by Dr. Bateson and Professor Punnett, who were thus able to show that what is called reversion, the reappearance of some ancient racial trait lost, it may be, long ago, may take place if and when races bearing factors complementary to one another are mated. When the complementary factors meet in the zygote the long-lost character is re-evoked in the body of the offspring.

Yet another complication may be cited and elucidated because of its general physiological significance. Some plants —Chinese primula, foxglove, &c.—have two kinds of white flowers. One, the ordinary kind, lacking the factor for colour, is known as a recessive white. When crossed with a coloured race it gives a coloured F_1, because, even though only one parent contributes the factor for colour, the presence of the single factor suffices for colour-production. The other kind of white behaves differently. Crossed with a coloured race it gives a white F_1. The explanation, confirmed by breeding experiments, is that the whiteness in this case is due to a factor which inhibits, that is, puts a veto on, colour-formation. Races which carry this factor are termed dominant-whites. If I stand for inhibitor of colour and C for the colour-producing factor, the factorial composition of a homozygous dominant-white race which carries the colour-factor is IICC, and that of a homozygous race with coloured flowers iiCC. The result of crossing the two is :

Parents :	Dominant-White	×	Coloured
	IICC	×	iiCC
Gametes :	IC	×	iC
F_1	IiCC	=	white

Gametes :



F_2 1 IICC, 2 IiCC, 1 iiCC

3 dominant-white : 1 coloured

Hitherto attention has been confined to the inheritance of a single pair of Mendelian characters; but now the behaviour in inheritance of two distinct pairs of characters must be considered. Those already investigated separately, namely, the leaf-shape and flower-colour characters of the Chinese primula, will serve as well as any others for the purposes of the investigation. If two races of Chinese primula, one breeding true to palm-leaf and coloured flower, the other breeding true to fern-leaf and white (recessive white) flower be crossed with one another, it is found that the members of the F_1 generation all bear palm-leaves and coloured flowers: the F_1 generation exhibits both dominant characters. An identical result is obtained if the cross be made between two races, one of which bears and breeds true to palm-leaf and white (recessive white) flower and the other to fern-leaf and coloured flower. Despite the difference in general appearance of the parents in the two cases the F_1 plants resulting from the two crosses are identical so far as these characters are concerned. How this comes about is evident when the genetical composition of the parents and of the F_1 generation is considered. In the former cross the parents are:

	Palm; coloured.		Fern; white.
	DD CC		dd cc
Gametes:	DC	×	dc
		|	
F_1		Dd Cc	

In the latter case the parents are:

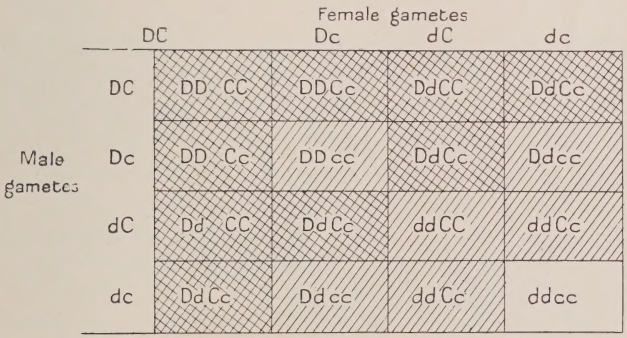
	Palm; white.		Fern; coloured.
	DDcc		ddCC
Gametes:	Dc	×	dC
		|	
F_1		DdCc	

Thus it is clear that not general appearance but factorial composition determines the course of heredity. If the F_1

plants raised as a result of either of these crosses be self-fertilized or crossed with one another, the gametes which are produced should be of the constitution :

(F_1 Dd Cc)
Gametes : DC
Dc
dC
dc

Now if the assumptions be made, first that each of these kinds of male and female gamete is produced in large and



approximately equal numbers, and second that a male gamete of any one type of constitution mates with equal readiness with any type of female gamete, the result in F_2 may be predicted. A simple method of presenting the matings and the constitutions of the F_2 zygotes which result from them is illustrated in the accompanying diagram. In it the constitution of the gametes is indicated along two sides of the large ' square ' and that of the zygote produced by the mating of each kind of male with each kind of female gamete by the letters in each of the small compartments. The different types of F_2 zygote are indicated by different shading : those with both dominants, D and C, are doubly shaded ; and so on.

As the diagram indicates, 16 matings are required to satisfy all the possible pairings of male and female gametes. Of the 16 F_2 individuals thus produced there should be :

9 (DC) which carry both D and C factors.
3 (Dc) ,, ,, D but not C
3 (dC) ,, ,, C ,, ,, D
1 (dc) ,, carries neither D nor C.

That is, in an F_2 family of 16 individuals there should be on the average—

9 DC, 3 Dc, 3 dC, 1 dc.
=9 Palm coloured, 3 Palm white, 3 Fern coloured, 1 Fern white.

Experiments involving the raising of large numbers of F_2 plants obtained as a result of crossing two races differing with respect to these two characters demonstrate that this ratio is obtained ; and breeding experiments with F_2 plants belonging to each of these categories demonstrate also that the members of the several categories have actually the composition ascribed to them. Thus it may be and has been shown that of the nine plants carrying both D and C there are those of the following constitution :

1. DDCC which breeds true.
2. DdCC which give in F_3 : 3 DC : 1 dC
   i. e. 3 Palm coloured : 1 Fern coloured
2. DDCc which give in F_3 : 3 DC : 1 Dc
   i. e. 3 Palm coloured : 1 Palm white
4. DdCc which behave like the F_2 plants

and so on for the other categories.

It is thus demonstrated experimentally that characters belonging to distinct Mendelian pairs segregate independently of one another, and it may therefore be concluded that the factors which give expression to one character and those which give expression to another undergo independent assortment. If, as may be supposed, each maternal and

paternal pair of chromosomes behaves during meiosis as an independent unit and separates into its maternal and paternal constituent independently of the other chromosomes, then the results which are obtained experimentally receive a reasonable interpretation. Any one aware of the complexity of living things will be prepared to believe that the results of the investigation of the inheritance of two pairs of characters do not always follow the simple (dihybrid) 9 : 3 : 3 : 1 scheme. But where complications arise the cytologist is ready with an explanation, though to consider here the nature of the explanation is unnecessary, inasmuch as it is dealt with in another volume of this series (*Animal Biology*, by Haldane and Huxley).

Practical consequences of great importance follow from the proved fact of the independent assortment of the factors for different Mendelian characters. Thus a race of wheat may be prolific yet a ready prey to attack by a certain species of rust fungus. Another may resist the rust yet yield poorly. By crossing the two races together it may be discovered whether prolificness and poverty of yield, rust-susceptibility and rust-resistance are Mendelian characters, how they are inherited, and whether it is possible to combine the desirable characters in one and the same race. The attempt has been made. It has proved successful and there are now flourishing in our fields varieties which combine the heavy-yielding character of one of the parent races with the rust-resistance of the other. By similar Mendelian methods other races of wheat have been raised which combine 'strength' of flour with heaviness of yield. The former quality, which expresses itself in a shapely, upstanding, and voluminous loaf as opposed to the unshapely and shrunken loaf made from weak flour, has been combined with prolificness with the result that British farmers, who formerly had to be content to grow high-yielding wheats which owing to lack of strength were not very suitable for the modern bakehouse, may now grow varieties which are both strong and high yielding. Thus it is that,

thanks to the pioneer work of Mendel, plant-breeding has become one of the chief methods whereby the economic value and range of cultivation of farm and garden plants may be augmented.

The task with which this chapter was charged is now done. It has given a glimpse of the Mendelian threads out of which the fabric of life is woven and by which that fabric is maintained and renewed. The larger enterprise, to inquire into the nature of variation, and to consider the part played by natural selection or the influence of environment in evolution, may be left to the authors of the companion volume on the lives of animals: great themes—to search out for the propulsive force which has driven, and yet drives, organism on its eventful evolutionary voyages, and to scan the heavens to discover what may be the star whereby evolution has steered its immemorial course.

IX

The plant commonwealth and its government; the integration of the plant; the sensitive plant (Mimosa pudica); stimulus and excitation; receptors and effectors; the transmission of excitation; chemical messengers (hormones).

The relations between the members of an individual plant resemble those which subsist between the members of a commonwealth of nations. The Free States of a commonwealth enjoy a large measure of unfettered liberty and so do the members of the plant commonwealth.

As the States are bound to one another by common ties of kinship and of custom, so are the members of the plant body. In consequence of these ties, and without affront to their liberty, the nations of a commonwealth act in concert and the commonwealth presents an united front to the world. In like manner the members of the individual plant are so bound together that their several activities exhibit a concerted orderliness, and the plant, notwithstanding the number and diversity of its members, appears and behaves as an individual. The unit of a commonwealth of nations is the individual citizen, that of the plant commonwealth is the cell. The living cell has, like man himself, a certain individuality; and like man, though it constitutes a unit, the cell is by no means simple but of very complex organization. The cell or protoplast is alive: it feeds, increases in substance, respires, may exhibit active movement, and may divide to give rise to new cells. As the individuality of the human being, even though strongly asserted, yet nevertheless merges in that of the nation, and as the national individuality is merged in that of the commonwealth, so the individuality of cells is merged in

that of the members of which they are constituents, and the individuality of the members in the larger individuality of the plant commonwealth.

In the simplest plants, composed of one protoplast, the cell is the individual. When it divides, the two cells to which it gives rise separate from one another and become each a new individual. In the higher plants also, in the beginning of their life-history, the individual is a single cell. Presently, however, this cell—the unicellular zygote, that is, the fertilized egg-cell —undergoes division ; but instead of achieving independence, the two daughter-cells, each surrounded by a continuous wall of cell-wall substance, remain united with one another. Similarly, when the daughter-cells divide, the four granddaughter cells remain united, and so by successive divisions the adult plant is established as a multicellular organism. Although housed each within its cell-wall the cells are not isolated from one another. The cellulose walls cloistering each protoplast are so thin and permeable that substances secreted by one cell may diffuse across them, and reach other cells. There are, moreover, living bonds of union between the cells of the plant. Fine strands, radiating from the cytoplasm, penetrate into pits in the cell-wall and join, or almost join, with corresponding strands from the cytoplasm of contiguous cells. As a result of this continuity of protoplasm even highly indiffusible substances—as, for example, enzymes—may be distributed from cell to cell. It is, therefore, not surprising to find that no cell of a multicellular organism lives unto itself alone. Each enjoys a certain freedom of action ; but on each cell is imposed a measure of social obligation. Out of the compromise between liberty and obligation arises the individuality of the members and the larger individuality of the plant commonwealth.

The individuality of the plant, though real, is less absolute than that of any of the higher animals. The difference may be likened to that which distinguishes a commonwealth from an empire. A commonwealth of nations leaves more liberty

to the associated members. They may even withdraw from the confederation, but in an empire the attempt to withdraw leads to widespread trouble, and when unsuccessful is called rebellion. A cutting taken from a plant may strike root and reconstitute an individual, and the separation does no permanent harm to the parent plant. In some cases—e. g. dandelion and seakale, &c.—a whole plant may be regenerated from a piece, no broader nor thicker than a sixpence, taken from the root, and plants are known which have such vigorous powers of regeneration that one single cell of leaf or stem whilst still in its place in the plant may assume the powers of a fertilized egg-cell and begin and continue to divide and grow until it forms a bud which, becoming detached, strikes root and develops into an independent plant. In such manner, as has been described already, a single cell of the leaf of certain species of begonia may give rise to a new plant.

Again, although, in natural conditions, the life and growth of roots depend on the supply of food-materials reaching them from leaf and stem, a root detached from a stem and placed in a suitable nutrient medium consisting of sugar and mineral salts, may remain alive, increase in length and thickness, and go on forming woody tissues and lateral roots very much as it would have done had it remained attached to the stem. Even a detached piece of root-tip little more than one twenty-fifth of an inch in length, if supplied with all the food-materials it requires—certain proteins, sugar, and mineral salts—may go on growing. Its cells undergo division and give rise to the various tissues which it is the custom for roots to produce.

Nevertheless, in spite of the powers of independent growth and development which members of the plant commonwealth retain, the plant does still constitute an individual in which all the parts maintain due and appropriate order with respect to one another. The behaviour of the leading shoot of a pine tree, referred to on p. 137, illustrates the subordination of the activity of the parts to the interests of the whole plant. The leader consists of a terminal bud beneath which is a whorl

of lateral buds. In ordinary circumstances, when growth begins in the spring, the terminal bud elongates and forms a stem which grows vertically upward and the lateral buds grow out more or less horizontally to form a whorl of branches. But if by accident or design the terminal bud is destroyed, one of the lateral buds may assume the lead. The shoot which it forms no longer grows out horizontally as part of the whorl of lateral branches, but, rising up vertically, takes the place of the lost leader. It is therefore evident that there are processes at work in the plant making for oneness or individuality. They may be described as processes of integration, and the subject of paramount interest in plant physiology is the nature of the integrating or unifying processes.

The existence in the higher plants of an elaborate system of transport whereby water and mineral salts are carried to the leaves, and sugars and other food-materials are distributed from the leaves to other parts of the stem and root, is in itself evidence both of the existence and the efficiency of integrating processes. As the quality of its roads and other ways of communication indicates, in a measure, the state of social development of human communities, so may the efficiency of their systems of communications serve as an index of the evolutionary status of plants, for of the one and the other it is alike true that evil communications corrupt good commonwealths.

The integrating processes which make for oneness in the plant consist by no means chiefly in the elaboration of transport service. The ties which bind together the nations of a commonwealth ' are trifles light as air but strong as iron ' ; and not less subtle nor less strong are those which unite the cells into tissues and tissues into members, and subordinate the members to the general interests of the plant commonwealth.

How subtle are the ties which make for unity may be judged by the behaviour of any one of those sensitive plants such as *Mimosa pudica* (Fig. 49), which, when stimulated, show their individuality by manifest and orderly movements

of the leaves. If a sensitive plant be growing actively, and the day be warm and sunny, a slight shock causes the leaflets to fold up and the leaf-stalks to hang down. When, for

Fig. 49. Sensitive plant (*Mimosa pudica*), showing the leaves in the normal position and after stimulation (see text).

example, the rays of the sun are focused by means of a burning-glass on a single leaflet, the pair of leaflets of which it is one fold together, and then the next pair, and so on until all the pairs of leaflets that form part of that section of the compound

leaf have folded. Then the stalk which bears the folded and depending leaflets drops sharply and droops down. The commotion, still spreading, affects the other parts of the leaf and their leaf-stalks in similar manner, until at last the main leaf-stalk drops suddenly and the whole leaf presents a distressful aspect (Fig. 49).

It is evident from this sequence of events that a local and by no means mortal shock induces far-reaching and orderly results. Any disturbance—that is, change in external conditions—which evokes a response may be spoken of as a stimulus. The immediate effect of stimulation is a local change in the tissues on which the stimulus acts. The change may be termed an excitation. The ultimate result of excitation, in the case just described, is a movement of leaflets and leaf-stalks. The stimulated tissues emit a message which is transmitted along the tracts intervening between the part of the plant which receives the stimulus—the receptor—and the parts which respond to it—the effectors.

In order to analyse the behaviour of the sensitive plant more thoroughly and at the same time to explore the nature of the integrating processes which make for uniformity of behaviour, the results following from stimulation of the main root may be studied. If the root be cut, without shaking or otherwise directly stimulating the stem, the leaves maintain for a time their natural positions. Presently, however, the lowermost leaf folds its pairs of leaflets and points its lateral and main leaf-stalks steeply down. After an interval the next leaf follows suit, folds its leaflets, and lowers its leaf-stalks to the ' half-mast ' position, and then the next, and so on until all the leaves have responded to the effects of stimulation of the root.

The nature of the movement is not difficult to discover, but, until recently, the nature of the message which brings about the movement remained obscure. At the base of each main and lateral leaf-stalk is a swollen leaf-cushion or pulvinus. The cells of the lower side of the pulvinus are thin-walled : those on the upper side thick-walled. In normal conditions

the cells of the pulvinus are distended with water, and naturally the thin-walled cells are distended most. Their turgidity suffices to hold up the leaf-stalk, and each leaflet is similarly held up by the turgid cells in the lower half of the pulvinus at its base. On stimulation, the cells of the lower half of the pulvinus lose water which escapes into the intercellular spaces between the cells. The lower half of the pulvinus, becoming less turgid, can no longer sustain the leaf. Somewhat like a door which swings on its own hinges and closes by its own

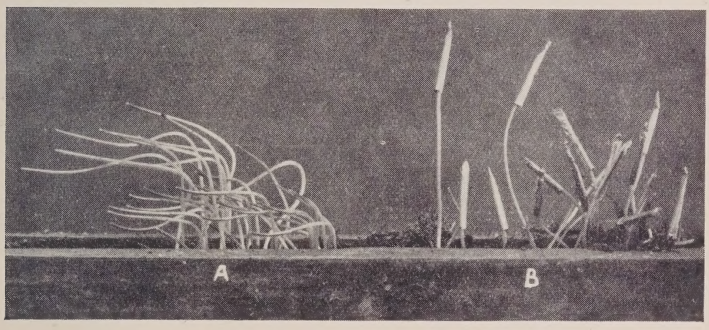


FIG. 50. Seedlings of the grass *Phalaris canariensis* submitted to phototropic stimulation (see text). A, with tip uncovered; B, with tip covered.

weight, the leaf-stalk swings downwards, hinging on its pulvinus. The relatively slow and successive movement of the leaves suggests that the message travels along the root upwards through the stem, and is delivered at the leaves successively. The track along which the message passes may be discovered by experiment. If epidermis, cortex, and bast be cut away, the leaves continue to respond to injury of the main root, and so they do when nothing is left for the message to pass along but a bridge of woody tissue. Somehow then, in some form or other, the message passes along the wood. Further experiment reveals the fact that it is carried by a messenger. The messenger passes, even though the elements of the wood be killed by anaesthetics or by heat. When, for

instance, a short length of stem is heated above the death-point of its tissues, the leaves outside the injured region remain fresh for some time because water from the root still reaches them, and so also may the messenger reach them ; for if now the root be cut the leaves fold as before. The kind of messenger which bears the message may also be discovered. If before the root is stimulated the stem is cut in two, and a short length of glass tube filled with water be used to connect the severed ends, the plant recovers for a time from the operation. When its leaves are outspread once more they may be caused to fold and fall again by section of the root. The messenger, therefore, is a specific chemical substance liberated as a result of stimulation, as for example by cutting the woody tissues of the root. The chemical messenger or *hormone* is carried in the transpiration stream along the woody vessels and as it passes knocks, as it were, at each successive leaf. The effect of the arrival of the messenger is to cause the turgid cells of the pulvini to excrete water, and thereby to lose their power of bearing up the leaf-stalks and the leaflets.

Although this is by no means the whole secret of the sensitiveness of *Mimosa pudica*, it suffices to show how integration of behaviour of the leafy members of the plant is brought about, and to suggest the means whereby integration in plants generally is effected. For it is not to be supposed that the method of excitation by specific chemical excitants or hormones is peculiar to the sensitive plant. It is common to all plants.

Among the stimuli to which plants respond with great readiness are those set up by change in the direction in which light falls upon them, and by change of position with respect to the vertical. The responses evinced by light- and gravity-stimuli are known respectively as heliotropic (phototropic) and geotropic movements. In the case of root and stem the responsive movement of curvature is generally brought about by a change in the relative rate of growth of the two sides of the elongating region of the tropistic

member. A root laid on its side gradually curves downward by the unequal growth of the two sides of its elongating region until its tip is once again vertical. The young leaf of a grass—e. g. an oat seedling—the tip of which is illuminated from one side, undergoes a disturbance of growth. The elongating lower part of the leaf grows faster on the side away from the light, and thereby the tip is brought to point again toward the light. A field of corn battered down by storms of wind and rain in summer presents a sad sight, with all the corn stems prostrate on the ground. But if the corn be not too ripe it may recover and every stalk stand once more upright. The storm drove the stems out of their course ; each was laid horizontally on the ground. In the prostrate state, the swollen nodes of the stalks lie athwart the line of action of gravity, and in this position are subjected automatically to geotropic stimulation. As a result they begin to grow again, and, growing more on the under than on the upper side, each sharply bending node sets the stalk once more on its vertical course. Once the stems are re-established in the vertical position, gravity ceases from troubling and the upright plants are at rest. In this position the nodes, remaining unstimulated, no longer grow faster on one side than on the other, and so the vertical course is maintained.

Every root pointing vertically downward, and every stem rising vertically upward, is a token of those exquisite powers of adjustment whereby the plant maintains its individuality and secures favourable working positions for its members. That this is so may be judged by the fact that, unlike a stem, a leaf of the ordinary type requires, if it is to take full advantage of sunlight, to lie in a plane more or less at right angles to the direction of the light. As every one knows, broad leaves generally do lie in this plane. Try to divert them from it and they bend or twist, and so in one way or another resume their natural position with respect to light. If they are illuminated from one side only, leaves turn by growth either of their blades

or stalks until the plane of the leaf-surface is once again approximately at right angles to the light. Moreover, if the blade be fixed so that it cannot move, the re-orientation may still be effected by curvature of the petiole.

In the sensitive plant a stimulus may be received by almost any part, root, stem, or leaf; but in those parts of plants which respond to the stimulus of light or gravity there is to be discovered a localization of the receptor—that is, the apparatus which registers the stimulus.

In the case of gravity-stimulation of roots it was long ago observed that the root-tip acts as the receptor. If, for example, the root-tip be cut away, the root when placed in a horizontal position shows no geotropic response, but continues to grow more or less horizontally (Fig. 51 B). That the loss of power to respond to the stimulus of gravity is due to the removal of the receptor, and not to any change in the transmitting- or in the effector-apparatus may be shown experimentally. The experiment may be carried out in a rough-and-ready manner without the aid of special apparatus, but it is more instructive if done with greater precision by means of the clinostat. This instrument consists of a clockwork or other mechanism which brings about a continuous and slow revolution of a horizontal axis. Seedling plants attached, for example, parallel to the axis are turned completely over at each revolution. In the course of the revolution the side which was directed upwards at the beginning faces downward when the axis has made a half revolution, and upward again when the revolution is complete. On the clinostat, therefore, the root or stem passes through a series of opposed positions with respect to the line of action of gravity, which, as it were, cancel out. In no position does the plant remain long enough to respond to stimulation by curvature. At each, the receptor receives the stimulus and undergoes a measure of excitation, but, before any effective message may be got off, the root, turned through 180°, is upside down. The receptor must, if it send anything now, transmit a message contradicting that which

it should have sent before, and so on all the way round. The upshot is that no messages are transmitted, and the slowly revolving plant shows no geotropic curvature. Root and stem, if straight at the start and if screened from the light, remain

FIG. 51. Response of root of broad bean (*Vicia Faba*) to geotropic stimulus. A, intact root showing positive geotropism ; B, decapitated root showing no geotropic response ; C, geotropic response by roots of which the root tips have been removed and replaced by means of gelatine (see text).

straight. They go on growing in the direction in which they were originally placed.

The clinostat is therefore very useful for the present purpose in that it prevents any chance geotropic stimulation. Nor is the likelihood of chance stimulation remote : for even though a root be placed only a degree or so out of the vertical its

geotropic curvature will record the misplacement with the certainty of a plumb-line. Seedlings of some sturdy plant—a sunflower or broad bean—grown in coco-nut fibre, with roots of about one inch to one and half inches in length, may be laid in pairs with their roots horizontal for a given time—say one pair for one minute, one for five minutes, one for ten, and one for fifteen minutes. After exposure in the horizontal position the root-tip is removed from one of each pair. At the end of the appointed time each seedling of a pair is attached to and revolved upon the clinostat. The apparatus is kept going for an hour or so, always revolving at a slow rate, say a revolution in twenty minutes. Inasmuch as no gravity-stimulus is effective when applied to the revolving plants, any well-marked and progressive curvature which appears in any of the seedlings must be attributed to the geotropic stimulation to which they were subjected before they were placed on the clinostat. It is not very long—a matter perhaps of five minutes—before the seedlings which were exposed horizontally for fifteen minutes begin to curve. After another five minutes or so the seedlings which received a ten-minutes' exposure also begin to curve, and even those which were exposed horizontally for only five minutes may presently show some curvature. Those which were horizontal for only one minute show none, no matter how long they are left on the clinostat. It is evident, therefore, that the receptor—the root-tip—must be presented to the stimulus for a certain minimum time for excitation to become effective in bringing about a motor response. This minimum time, known as presentation time, amounts, in the case of geotropic response, to from five to ten minutes according to the kind of plant and its state. Excitation, on the other hand, is all but instantaneous, but nevertheless the results of excitation must reach a certain amount before they are powerful enough to convey a message to the growing region and set that region curving. Hence it is that the seedlings stimulated for one minute show no curvature. The excitation dies away before it has developed enough strength to send out a message. Yet

excitation there was even during the one minute's exposure to gravity-stimulation, and this may be shown by the use of a clinostat so adjusted that it stops for a certain space of time —say one minute—at a certain point in its revolving course, and then resumes its revolution. If the rate of revolution be very slow, roots placed on the intermittent clinostat show no curvature. Each individual weak excitation which occurs during the short stoppage is washed out or extinguished. But if the rate of revolution, though still slow, is somewhat faster, so that the time-ratio of rest to revolution is not less than 1 : 5, something of the excitation persists when the clinostat stops again, and so the excitations sum themselves up until reaching a sufficient magnitude they encompass the sending out of a message which reaches the elongating region and is there taken in and acted upon : the root curves geotropically.

It may be shown by cutting off the root-tip from one of each of the pairs of seedlings used in the experiment with the continuous clinostat that the removal of the receptor, after its exposure to geotropic stimulation for a sufficient time, has no effect on the transmission of the excitation nor on the reaction. Whether amputated or not the roots of a pair behave similarly. If the intact root curves geotropically so does the decapitated root.

Thus it is possible to analyse geotropic response : stimulus, receptor, excitation ; piling up of results of excitation till a messenger strong enough to make the journey is brought into being, travelling of the messenger from receptor to effector region ; arrival there with a consequent bringing about of an interruption of the routine of cell-growth, which interruption is made manifest by the motor response ; the cells of the side which was upward during the horizontal exposure grow faster than those of the opposite side, and the side of which the faster-growing cells are part curves downward until the root-tip points again towards the centre of the earth.

Only one conclusion can be drawn from the behaviour of decapitated roots. Those decapitated before exposure to the

stimulus of gravity show no response. Those exposed to gravity-stimulation and then decapitated curve no less than do intact roots. Though the decapitated roots transmit the results of excitation and react by curvature, with the loss of the root-tip the power of receiving the stimulus is lost. It is therefore legitimate to conclude that the receptor for gravity-stimulation is localized in the root-tip.

Localization of receptor may be shown also to occur in parts of plants which respond to the stimulus of light. The seedlings of diverse grasses—oats, Phalaris, &c.—form a first, spear-like, imperfect leaf which is remarkably sensitive to light. Seedlings raised in a shallow box in darkness stand bolt upright. Brought into dim diffuse light some of the seedlings may be quickly 'blind-folded' by covering their tips with tin-foil twisted to form a little cap (Fig. 50, p. 231). If a dark room provided with a red light be available for the operation of capping so much the better, for red light is far less potent than blue or violet in inducing heliotropic curvature. Brought into the light and illuminated on one side only—e.g. by means of a large pinhole in a cardboard cover placed over the open side of the otherwise closed box of seedlings—all those plants which remained uncapped bend in such a way that the tip of each leaf points towards the pinhole. The capped plants, on the other hand, either remain erect, or show an ineffective, hesitating curvature which lacks altogether the precision of that of the uncapped plants. The result demonstrates that, as for the stimulus of gravity, so for that of light there is a localization of the receptor, and that not every part of a plant on which light falls is so affected as to be stirred to send precise and definite messages leading to precise and definite growth-curvatures of distant parts. Presently it will be necessary to say something more of receptors, but for the moment interest lies in the nature of the messages which they send forth.

When the receptors of the human body—as, for example, the sense-organs—are stimulated by appropriate change in the

external world, they register the change, undergo excitation, and send out messages. The messages, known as nervous impulses, pass along specialized conducting tracks, the nerves, and sooner or later bring into operation muscles, glands, or other effectors. A buzzing fly alighting on the nose is quickly, albeit often ineffectually, swept away by a movement of the hand.

With the knowledge of the part played by nerves in the transmission of the results of excitation it is natural that physiologists should seek in plants for the counterpart of the nerves of animals. The existence of localized receptors would seem to encourage the search, for they are analogous with the special sense-organs of animals. Nevertheless the search has so far proved vain. There are no structures in the plant which surely correspond with the nerves of animals. It is true that some have imagined that the fine protoplasmic fibres which connect cell with cell are nerves of a primitive kind, but although it is not possible to disprove the conjecture, it seems more probable that the fibres serve for chemical—that is, material—transmission from cell to cell rather than for the propagation of such physical messages as are the nervous impulses of animals.

In any case it is known that, as with the sensitive plant, so with other plants, stimulation may result in the formation of specific chemical substances which, acting as messengers between the receptor and the effector mechanism, cause the latter to initiate movement or other change in obedience to change in environment. If the tip of the first leaf of an oat seedling be cut off, one-sided illumination of the remaining part does not bring about heliotropic curvature ; but if the tip be replaced in position by means of a thin layer of gelatine, the seedling resumes the power of heliotropic response. One-sided illumination of the replaced tip leads to such curvature of the growing region that the tip is brought to point towards the light. It is therefore to be concluded that the excitation which follows upon unilateral illumina-

tion results in the production of a hormone in the receptor apparatus located in the tip of the seedling leaf, and that the hormone diffuses from the tip through the gelatine, reaches the motor region, and there provokes those changes in rate of growth of the two sides which bring about the curvature of the leaf. Why, however, the reception of the message should result in a difference in rate of growth on the two sides is obscure. It may be that different quantities of the hormone pass to the two different sides, and just as a little piece of bad news may be stimulating and a lot depressing, so different quantities of hormone may produce different results.

What is true of the heliotropic message is true also of the geotropic message. The one, like the other, is a chemical message. Removal of the root-tip results in the loss of geotropism. The receptor gone, the stimulus is not registered. But if the amputated tip be replaced and fixed in position by means of gelatine (cf. Fig. 51 C), exposure of the root to the stimulus of gravity leads, as before, to geotropic curvature: the 'reheaded' root curves until the tip points once more vertically downward.

Long before it was discovered that the purposeful responses of roots, stems, and leaves to the stimuli of light and gravity are brought about by chemical messages, it was known that certain other plant-movements are the result of chemical stimulation. The power of reacting to specific chemical substances is indeed manifested by many, if not all, lower organisms. An amoeba, for example, may be constrained to change the direction of its curious pseudopodial movement by placing in its neighbourhood a pellet of blotting-paper soaked in extract of meat. Stimulated by the substances diffusing from the extract, the amoeba throws out a protoplasmic projection (pseudopodium) in the direction of the pellet, and its body, flowing into the pseudopodium, presently comes to engulf the pellet, which may be seen lying in a vacuole in the body. If instead of extract of meat

the pellet be soaked in a solution of tannin, or of nitrate of silver, the amoeba gradually moves away from it.

Directive movements of free-moving organisms to or from specific chemical substances are known as chemotactic movements. Among the most striking examples of tactic response to chemical stimulation are those exhibited by the male reproductive cells of Mosses and Ferns. The cells, which are known as spermatozooids, consist each of a minute, unicellular, flagellated protoplast. The female reproductive cell, with which a spermatozooid must fuse if fertilization is to be effected, lies when ripe at the bottom of a minute, flask-shaped structure, the female reproductive organ (archegonium), the neck of which, open at its free end, is filled with a watery mucilaginous material. Into the neck of the archegonium spermatozooids find their way, and one of them, outdistancing its fellows, reaches the egg-cell and fuses with it. The way is found not by chance wandering, but by following a definite clue. The clue is a material one. From the neck of the archegonium a specific substance diffuses through the water-film which covers the plant on which the reproductive organs are borne. In that film the spermatozooids are swimming in aimless direction, until the messenger diffusing from the archegonium reaches them, and guides them ever towards the place of greater concentration until they reach the neck of the archegonium. By trying the effect of one chemical substance after another, it has been proved that the hormone excreted by the archegonium of Mosses is cane sugar and that of Ferns is malic acid.

In flowering plants also, power of response to specific chemical substances plays a part in the processes which intervene between pollination and fertilization, and between fertilization and ripening of seed and fruit. Although true of all plants, it is most easily demonstrated in those plants the flowers of which possess sensitive stigmas. *Mimulus cardinalis* is such a plant. It has a bilobed stigma. Gentle rubbing of the lobes causes them to close by folding together. So also

does the deposition of pollen on them. But the stigmatic lobes exhibit very different behaviours according to the kind of stimulus to which they are subjected. A few grains of sand or of dead pollen laid on the lobes cause them to fold together, but the lobes soon open out again. Similarly, if a little live pollen of other species be placed on them, the lobes fold up temporarily. If, on the other hand, a sufficiency of the plant's own pollen be put upon the stigma-lobes, they close and open no more. The interpretation of these different behaviours is that the lobes are sensitive to two kinds of stimuli. A mere rubbing of their sensitive surface—as, for example, by sand or pollen-grains—causes a closing movement. Response to contact, however, soon wears off and the lobes reopen. But the stigma is also sensitive to chemical stimulation, and if the stimulus be of the right kind and strong enough, the lobes, after performing the closing movement, are as it were narcotized and lose the power of opening, even after the effect of the contact stimulus has waned. That the lobes respond to chemical as well as to mechanical stimulation may be inferred from the fact that a watery extract of the pollen causes the stigma-lobes of *Mimulus cardinalis* to close and to remain closed.

In the course of the ripening of fruits, far-reaching changes often occur. The petals fade, the ovary swells, and its walls undergo structural alterations, some of which have already been described. It is wellnigh certain that all these changes are of the nature of responses to definite chemical substances of which some are secreted by the pollen and pollen-tubes. The flowers of not a few plants—for example, some Orchids—exhibit changes of colour as a result of fertilization. Some hybrids of *Cypripedium Leeanum* (Fig. 42, p. 195) have much white in their flowers, but after fertilization the white changes to canary yellow. Flowers of *Phalaenopsis Lueddemanniana* turn bright green after pollination. Yet more remarkable is the fact that flowers of *Oncidium flexuosum* are actually killed by the deposition of their own pollen on their stigmas. They

die for the cause of cross-pollination. Among common fruits may be found illustrations of the far-reaching effects of chemical stimulation. Some varieties of cucumber develop fruits even though they are not pollinated; but the fruits, which are seedless, are not so large as those which are produced by pollinated flowers. Moreover, if pollen be deposited on the stigma so sparingly that there are not enough grains to provide for the fertilization of all the ovules, the cucumber has a misshapen appearance, the stalk end—that is, the end farthest from the stigmas—remaining much thinner than the free end. Where pollen-grains failed to reach, the fruit failed to swell. Apples also have a misshapen form, if, as sometimes happens, some ovules escape fertilization. Growth of the sections of the fruit-wall neighbouring on the unfertilized ovules fails to keep pace with that of the sections which surround the fertilized ovules.

When all these instances of chemical stimulation are considered there can be no doubt but that the chemical messages which are transmitted by the plant from one member or tissue to another are numerous and potent. They play a great part in effecting co-ordination—that is, in promoting the unity and individuality of the plant. The most recent discoveries confirm this conclusion. It is a well-known fact that many parts of plants, although they are composed of cells which in normal circumstances would never divide again, if stimulated—as, for example, by mechanical injury—resume the power of division and give rise to new tissues. Many garden plants are regularly propagated by cuttings; short lengths of the stem taken from them strike root and reproduce the original plant. With some plants—as, for example, anchusas and Oriental poppies—root-cuttings serve equally well, or even better; and occasionally, as with begonias, gloxinias, &c., vegetative propagation by leaf-cuttings is practised. In all these cases regeneration is complete. The stem-cutting, after healing its wounded surface, produces adventitious roots. The root-cuttings develop adventitious buds, and, it

may be, also new roots, the former from the organically upper end and the latter from the lower end.

Not all the parts of a plant, however, are equally capable of regenerating new members. Whereas some trees—willows, for example—when polled may develop adventitious shoots, others, when a branch is lopped, can do no more than heal the cut surface. The healing process is complicated, and with a large branch so slow that it may take many years before the exposed surface is completely covered by ring after ring of woody tissue encroaching gradually toward the centre of woody elements, and produced in the main by the activity of the cambium beneath the cut surface. Other parts of plants show even less power of regeneration after mechanical injury. All they can do is to heal the wound by the formation of layers of cork. The cells injured by the cut wither and die. One or more layers of cells beneath the withered surface resume power of division. Each cell divides by walls parallel to the free surface to form a vertical row of three or four cells. The middle cell or cells of each tier assume a regular brick-shaped form, and, since all the cells divide at about the same rate, the layer of brick-shaped cells may be continuous, like a wall, right across the wounded tissue just beneath the surface. The layer of cells thus formed is known as cork-cambium. Each cell is thin-walled, nucleated, and rich in cytoplasm. The cork-cambium cells divide and redivide transversely, so that from each an increasing tier of brick-shaped cells is formed. The lower retain the power of division, but the more superficial layers of cells lose cytoplasm and nucleus, and as they die secrete corky substance (suberin) in and on their walls, so that ultimately a layer of cork is formed, and thereby the delicate tissues beneath the wounded surface are protected from desiccation and the wound is healed.

The formation of cork following upon injury is of widespread occurrence in plants. Sometimes it occurs as the result of attack by parasitic fungi, and then the botanist, aided by the microscope, may witness a protracted struggle between

parasite and host plant. As the fungus penetrates deeper into the tissues of leaf or stem, chemical warning of its approach is given to the as yet intact or scarcely affected cells. They 'respond' to the message by forming corky layers, and the life of the plant may depend on which is the winner—the attacking fungus or the defending tissues of the plant. Thus, for example, larch cankers reveal that the tree attacked is no mere passive victim to the canker fungus, but puts up, as it were, a running fight, erecting a series of corky barricades to check the advance of the invading fungus.

A similar method of protection against imminent adverse conditions of climate is practised every year by most of our trees and shrubs. Each year in late summer, and long before the weather gives any hint that winter impends, the plants form corky layers, which may be cast off each spring, or accumulating year by year give rise to thick and rugged bark.

What signal gives the message in time for cork to be formed and finished before winter begins is not known. It may be that soil-temperature, which in this country begins to fall in June, sets going a train of events which leads to messages reaching the tissues destined to form cork, and stimulating them to begin their work. Or it may be that the ever-increasing pressure exerted by the expanding woody cylinder fires the train. The example now to be given would perhaps suggest that the latter is the true explanation. In some parts of plants—potato tubers and swollen stems of turnip-rooted cabbage (Kohl-rabi)—cork formation follows on a cut. The formation of cork may, however, be suppressed partly or entirely by washing the wound very thoroughly with running water. The wound thus cleansed does not heal well, but, in the case of the Kohl-rabi, it may be made to heal by the simple and, as it would seem, dirty process of smearing the exposed surface with the brayed debris of a part of the swollen stem. The cells beneath the wounded surface are quickened into activity by a chemical message which reaches them from the

wounded and dying cells. Washing the cells washes away the messenger. If uninterfered with, the last act of the mortally injured tissues is to form a 'wound-hormone'—a messenger of healing—which, diffusing from them, reaches the living cells beneath, and quickens them to renewed activity and division. Thus even in their death the stricken cells have care for the welfare of the plant commonwealth.

When all the facts concerning plant hormones are considered, it is difficult to escape the conclusion that the government of the plant commonwealth is carried out by means of chemical messages, and that whereas the animal body uses a twofold method of intercommunication, the plant body uses one method only. In animals the messages which are sent are of two kinds—quick messages along nerve fibres, comparable to telegraph messages sent to definite addresses along special lines, and slower material messages, hormones which the blood-stream delivers universally. But though the latter messages may reach all parts of it they are intelligible only to certain members of the body—that is, they only produce reactions in certain tissues: messages comparable to those contained in an imperfectly addressed letter which the postman carries with him on his rounds and presents at each door until, perchance, it is taken in by the household which is expecting it and recognizes the writing.

Whether indeed the strangely divergent destinies and shapes of animals and plants are to be traced to the complete lack in plants of anything resembling the nervous tracts of animals, it is at present impossible to assert; but this at least may be said with confidence, that, no less than in the animal world, chemical messages play a great part in determining plant-behaviour and in securing the unification of the plant commonwealth.

No one who has followed this story of plant-behaviour will entertain any longer the idea prevalent among men that plants lead a lethargic and very passive existence. It is clear that they, and all their parts, are incessantly in receipt of

messages which affect their activity. Living cells are always 'listening in', and their registering apparatus is so delicate that it may even receive messages of which we remain oblivious. Among the most delicate receptors are tendrils. A tendril of the passion-flower (*Passiflora gracilis*) may execute a curling movement when a thread of gossamer weighing no more than 1/4000 mg. is placed and sways upon it. To make us aware of its presence the thread must needs weigh ten times as much. The human eye is exquisitely apt to recognize the brighter of two sources of light. When young we see a difference of 1/100th, that is, the difference between a 100 and a 99 candle-power lamp. With increasing age vision becomes less acute, and only differences of 1/30th—e. g. those between a 100 and a 96·7 candle-power lamp—are to be recognized. A leaf of a plant may show by the orientation of its blade in response to one-sided illumination that it registers a difference of 1/75th—that is, the difference between a 100 and a 98·5 candle-power lamp. Again, although the human eye is marvellously sensitive, it is doubtful whether it is more so than the tip of the first leaf of an oat seedling. Sunlight enduring for so brief a space as 1/2000th of a second does not escape registration by the plant. Although the leaf exposed to light for this fraction of a second does not curve, yet it is easy to show that the change of environment has produced an effect on the receptor. For by exposing one side of the tip to sunlight and darkness alternately—each time of exposure to light being no longer than this brief time, provided that the intervening periods of exposure to darkness be not too long, the plant presently begins to curve just as it would have done had it been exposed continuously to unilateral sunlight. The receptor records each brief stimulus. Its living cells undergo excitation. The successive excitations, if they do not follow one another too slowly, sum themselves up, and, reaching a certain magnitude, evoke a message which, arriving at the effector, sets going in it the heliotropic curvature.

It is strange that so delicate a registering apparatus as that contained in the tip of the seedling oat-leaf should, even when the leaf is examined microscopically, give no hint of the manner of its construction. But so it is. Nevertheless something has been discovered of other of the plant's receptors. For example, the receptor in the tip of roots which registers change of position is located in the tissues of the root-cap. The cells of the series of layers which constitute the cap are nucleated and rich in protoplasm (Fig. 33, p. 135). They contain numerous starch grains, the behaviour of which is different from that of the general run of starch grains found in other parts of the plant. In accordance with its role as a reserve food-material, starch gradually disappears when green plants are starved—as, for instance, by keeping them in darkness. Not so the starch grains of the root-cap. They persist even after long starvation. So long as they persist the root is capable of geotropic response; but when the starch grains do disappear from the cells of the root-tip, power of geotropic response disappears likewise, and only reappears when new grains have been formed in the tip.

Another significant peculiarity of the starch grains of the root-tip is their mobility. In general the starch grains contained in plant-cells are so embedded in the cytoplasm that they do not readily undergo change of position; but those of the root-tip are so mobile that any change of position of the root with respect to the vertical brings about a movement of the starch grains of the root-cap. Like marbles on a board which roll down when the board is inclined, the movable starch grains roll down whenever the wall on which they lie takes on even a slight slope.

In animals—e. g. Crustacea, &c.—balancing and orientation are brought about by specialized receptors known as statocysts. A statocyst consists essentially of a minute, hollow, cytoplasmic sphere. Within the spherical space is contained a statolith—a mass of chalk or other solid substance. With each movement of the animal the statolith rolls on to another part of the living

floor. There are good reasons for believing that the deformation of a given area of the cytoplasm set up by the pressure of the statolith upon it is the origin of the excitation which results in appropriate movements of adjustment. When the statocyst consists of one cell it may be called a statocyte, which term botanists have appropriated and applied to what appear to be similar receptors, the starch-containing cells of the root-tip. Nor indeed need the 'statolith' consist of starch. In some plants—e. g. Grasses—the haulms are very sensitive to displacement from the vertical, and in the nodes of the haulms both starch grains and also minute crystals of calcium oxalate occur in certain of the groups of cells concerned in receiving the stimulus of gravity.

Ingenious investigators have also claimed to have discovered the nature of the receptor-apparatus in leaves which registers change in direction of light, and thereby sets going the chain of events which leads ultimately to a readjustment of the leaf-surface, so that the leaf comes once again to lie at right angles to the light. The receptors, or ocelli, consist each of a surface-cell, the outer wall of which, being convex, acts as a lens focusing a spot of light on the basal wall of the cell. When light falls vertically on a horizontal leaf the 'spot' is centred on the basal wall of each epidermal cell, and when this is so no excitation follows. But if light fall obliquely on the leaf the spots are no longer centred, but lie to one side of the centre. The displacement suffices, or is supposed to suffice, for a registration of the stimulus and for the excitation which ultimately leads to a movement of adjustment.

In certain tendrils, but not in all, minute pits occur in the outer walls of some of the superficial cells, and their mode of action may perhaps be compared with the behaviour of the stretched parchment or skin of a drum. As a slight touch on the latter sets up much reverberation, so the merest pressure on the thin places of the cell-wall is communicated to the cytoplasm which lines the pit and acts as a receptor. Similarly in other highly sensitive structures—e. g. the stamens of *Berberis*, &c.,

and the bristles of Venus' fly-trap (*Dionaea muscipula*) and other insectivorous plants somewhat similar sounding-board arrangements—thin places in the walls of certain cells—serve in all probability to enable the sensitive cytoplasm which lies beneath them to register stimuli and so initiate movements.

This brief study of plant receptors illustrates the exquisite sensitiveness of cytoplasm and the variety of stimuli to which plant protoplasm responds. The stimuli are the signposts by which the plant keeps the even tenor of its way. A little straying from the path and the warning signal is given and the vagrant plant returns: as a cyclist pursues a straight path by a series of compensating wobbles, so does the plant. By keeping constant touch with the outside world, and by its several parts maintaining chemical touch with one another, the plant commonwealth establishes and maintains itself so surely and so harmoniously that every member of it would seem to live a life of effortless ease. But the penetrating eye of the poet no less than the patient eye of the man of science has seen the incessant surge of activity by which life aspires and living things evolve.

> Behold the life of ease, it drifts . . .
> The sharpened life commands its course.

INDEX

A

absciss layer, 139.
Acer pseudoplatanus, 8.
Acetic acid bacteria, 148.
adsorption, 108, 113.
adventitious roots, 35.
Aesculus hippocastanum, 6.
Alder, 8.
aleurone layer, 36, 132.
Algae, 22, 23.
alkaloids, 133.
Allium porrum, 88.
Alnus glutinosa, 8.
American water-weed, 79, 193.
amino-acids, 85.
amoeba, 240.
anaerobes, 143.
anaerobic respiration, 143.
Angiosperms, 126.
annual rings, 125.
annuals, 40, 139.
annular vessels, 128.
anthers, 196.
anthocyan, 75.
apples, development of fruit of, 243.
archegonium, 241.
artificial manures, 178.
ascent of sap, 184.
ash (plant), 47.
asparagin, 86.
autotrophic plants, 150.
autumn wood, 125.
Azotobacter, 150.

B

Bacteria, 23.
Bacterium radicicola, 54.
balanced reactions, 113.
Bamboo, growth of, 136.
bark, 120, 245.
bark, secondary, 124.
Barley, germination of, 31.
bast, 124.
Beech, 8.
Begonia, 138, 227.
benthos, 1, 14, 22.
Berberis, irritable stamens of, 249.
bleeding pressure, 186.
Broad bean, 38.
Broom-rape, 156.
Brown bird-nest, 152.
Bryophyta, 22.
bud, 5.
bud-scales, 5, 8.
Butterwort, 19.

C

Cactaceae, 182.
callus, 129.
calories, 42.
calyx, 194.
cambium, 124.
cane sugar, 83, 92.
carbohydrates, 92.
  transport of, 146.
carbon assimilation, 81.
carbon dioxide, absorption of, 59.
  diffusion of, 65.
carotin, 75.
catalysts, 111, 141.
catalytic action, 111.
cell, 11, 103.
cell division, 203.
cellulose, 92.
cell-wall, 12.
central cylinder, 118.
chemotactic movements, 241
Chinese primula, 212.
Chlamydomonas, 12, 151, 190.

chlorophyll, 11, 23.
  composition of, 75.
  formation of, 69.
  absorption of light by, 69.
chloroplast, 24, 70, 73, 163.
chlorosis, 51.
chromosomes, 204.
clay, colloidal properties of, 107.
clinostat, 234.
Clostrydium pasteurianum, 150.
coagulation of proteins, 107.
coal, 3.
colloids, 106.
Colocasia, 168.
companion cells, 128.
Convoluta rosscoffensis, 152.
cork, 120, 244.
cork-cambium, 244.
Cork Oak, 180.
Cornus sanguinea, 6.
corolla, 194.
cortex, 118.
Cotyledons, 33, 38.
cross-pollination, 194.
crystalloids, 106.
Cucumber, 243.
Cuscuta europaea, 157.
cutin, 62.
cuttings, 243.
Cypripedium Leeanum, 195, 242.
cytase, 115.
cytoplasm, 11.

D

Date-palm, 68.
dextrose, 83, 92.
diastase, 112.
Dicotyledons, 33.
differentiation, 134.
diffusion, 65, 97, 115.
Dionaea muscipula, 154, 250.
diploid (number of chromosomes), 208.
di-saccharides, 96.
dispersal of seeds, 202.
Dodder, 157.
Dog mercury, 17.
Dogwood, 6.
dominance, 215, 218.
dominant-white flowers, 219.
double fertilization, 201.
Drosera rotundifolia, 19, 154.

E

effectors, 230.
egg-cell, 200.
Elodea canadensis, 79, 193.
embryo, 31.
embryonic cells, 135.
embryonic organs, 32.
emulsoids, 106.
endosperm, 36, 201.
endosperm nucleus, 201.
enzymes, 111, 115.
  colloidal properties of, 112.
epidermis, 62, 118, 161.
etiolation, 35.
Eucalyptus, 184.
Euglena, 12.
evolution, 190.
excitation, 230, 236.
exosmosis, 101.
eye-spot, 11.

F

factors, Mendelian, 214.
Fagus sylvatica, 8.
fat-splitting enzymes, 145.
fermentation, 143.
Ferns, 22.
  male reproductive cells of, 241
fertilization, 193, 200.
Ficus elastica, 172.
fixation of nitrogen, 55.
flagellum, 11.
floral mechanisms, 193.
Flowering currant, 8.
formaldehyde, 82.
fossil plants, 2, 189.
fruit, 202.
  ripening of, 242.
Fucus platycarpus, 15.
Fungi, 23, 26.

G

gametes, 192, 200.
Genetics, 211.
geotropic response, 233.
geotropism, 232.
germination, 31.
Ginkgo biloba, 190.
glucosidal enzymes, 134.
glucosides, 134.
Gorse, 180, 196.
grassland, 17.
Grass wrack, 19.

growing-point, of stem, 122.
growth, 134.
growth of cell-wall, 136.
guard-cells, 63, 163.

H

haploid (number of chromosomes), 208.
healing of wounds, 244.
heliotropic curvature, 238.
heliotropism, 232.
  of leaves, 233.
herbaceous plants, 18.
heredity, 190.
  material basis of, 203.
heterotrophic plants, 150.
heterozygous, 215.
homozygous, 215.
hormones, 232, 246.
Horse-chestnut, 6, 8.
House-leek, the, 180.
hybrids, 198.
Hydrangea sp., 182.
hydrolysis, 95, 111.
hypha, 25.

I

imbibition (by colloids), 114.
Impatiens noli-me-tangere, 58.
India-rubber plant, 172.
inheritance of Mendelian characters, 220.
inhibitory factors, 219.
insectivorous plants, 154, 250.
integration (of plant behaviour), 225.
integuments, 199.
intercellular spaces, 65.
inversion of sucrose, 95, 111.
invertase, 111.

K

Kohl-rabi, 245.

L

laevulose, 110.
lamina, 6.
land reclamation, 55.
Lathyrus odoratus, 218.
leaf, 6.
leaf-base, 6, 8.
leaf-cuttings, 243.
leaf-fall, 139.
Leek, 88.
leguminous plants, 52.
leucoplasts, 72.
Lichens, 1, 152.
light and chlorophyll formation, 69, 73.
  influence on transpiration, 69.
  and on movement of chloroplasts, 73.
  and starch formation, 77.
lignin, 128.
Ligustrum vulgare, 8.
Lilac, 8.
lipase, 115.
Louse-wort, the, 157.

M

macrotherms, 18.
Maiden-hair tree, 190.
maltase, 115.
maltose, 115.
Maple, 8.
Marram grass, 18.
medullary rays, 118.
meiosis, 209.
Mendel, Gregor, 211.
Mendelian characters, 212.
  inheritance, 216.
Mercurialis perennis, 17.
mesotherms, 18.
micropyle, 199.
micro-species, 188.
microtherms, 18.
Mimosa pudica, 179, 228.
Mimulus cardinalis, 241.
Mistletoe, 154.
mitosis, 208.
monocarpic plants, 41.
Monocotyledons, 33.
monosaccharides, 96.
Monotropa hypopitys, 152.
Mosses, 22.
  male reproductive cells of, 241
mycelium, 26.

N

nectar, 168, 194.
Neottia nidus-avis, 152.
Nepenthes, 154.
nerves, 239.

nitrate of soda, 34, 52, 178.
nitrates, 21, 85, 87.
nitrifying bacteria, 28, 89, 148.
nitrogen cycle, 28.
nitrogen-fixing bacteria, 54, 87, 150.
nodules, root, 53.
nodule-organism, 150.
nuclear division, 204.
nucleus, 11.

O

Oak, 8.
ocelli, 249.
Oncidium flexuosum, 242.
optically active substances, 94.
Opuntia sp., 182.
orchids, 153, 193, 242.
Orobanche sp., 158.
osmosis, 100.
osmotic pressure, 100, 102, 184.
  substances, 100.
  system of vegetable cells, 103.
Osmunda regalis, 161.
ovary, 196.
ovule, 196.
oxidases, 141.

P

palisade tissue, 70.
parasites, 23, 29.
parasitic fungi, 169.
parchment membrane, 98, 100.
Passiflora gracilis, 247.
Passion-flower, 247.
Pasteur, 144.
Pea, 52, 196.
peat, 22.
Pedicularis sp., 157.
Penicillium, 144.
perennial plants, 41.
perianth, 194.
petals, 194.
petiole, 6.
Phalaenopsis Lueddemanniana, 242.
Phaseolus multiflorus, 179.
phloem, 124.
Phoenix dactylifera, 68.
photosynthesis, 81, 104.
Pine, growth of, 137, 227.
Pinguicula vulgaris, 19.
pistil, 196.
Pisum sativum, 196.
Pitcher plant, 154.
pith, 118.
plankton, 1, 11, 22.
plasmatic membrane, 102.
polarimeter, 94, 112.
polar nuclei, 200.
pollen, 196.
pollen-tube, 198.
pollination, 193.
polycarpic plants, 41.
polysaccharides, 96.
porometer, 171.
potometer, 173.
presentation time, 236.
primary vascular bundles, 121.
primary xylem, 123.
Primula sinensis, 212.
procambial strands, 122.
proteins, 21, 84, 87.
  systhesis of, 85, 89.
protein grains, 36.
proteolytic enzymes, 115.
protoplasm, continuity of, 226.
  streaming of, 116.
protoplast, 11, 226.
protoxylem, 123.
Pteridophyta, 22, 151.
pulvinus, 230.

Q

Quercus robur, 8.
Quercus suber, 180.

R

receptors, 230.
  localization of, 234, 238.
reduction division, 208.
regeneration, 227, 244.
reserve proteins, 87.
respiration, 140.
  stages of, 145.
respiratory enzymes, 142.
reversion, 219.
Ribes sanguineum, 8.
root, elongation of, 136.
  growth of, 227.
root-cap, 134.
  effect of amputation of, 237
root-hair cell, 103.
root-hairs, 56.

root-tip and geotropic response, 234.
Royal fern, 161.
Runner-bean, 179.
rust-resistance, 223.

S

Saccharomyces cerevisiae, 24.
Saccharomyces mycoderma, 148.
sand-cultures, 48.
saprophytes, 23, 147, 151, 152.
Sarracenia sp., 154.
Schizophyta, 23.
scutellum, 32.
Seaweeds, 14, 116.
secondary wood, 124.
seed-bearing plants, 22.
seed-coats, 199.
seed-leaf, 33.
seed-vessel, 196.
segregation, 214, 222.
selective adsorption, 109.
self-pollination, 196.
seminal roots, 31.
semi-permeability, 102, 110.
semi-permeable membranes, 101, 109.
Sempervivum, 180.
Sensitive plant, behaviour of, 230.
  movements of, 179, 228.
sepals, 194.
Sequoia gigantea, 126, 190.
sexual reproduction, 192, 207.
sieve-tubes, 123, 128, 130.
sleep movements, 179.
soil bacteria, 21.
soil-sterilization, 90.
soil-temperature, 245.
Spermaphyta, 22.
spermatozooids, 241.
Sphagnum, 19.
spindle-fibres, 204.
spiral vessels, 128.
spore, 24, 25.
sporophore, 26.
spring wood, 125.
stamens, 196.
starch, 36, 79, 83, 92, 164, 167, 248.
  formation of, 76.
  tests for, 77.
statocysts, 248.
statocyte, 249.
statolith, 248.
stem structure, 117.
stigma, 196.
stimulation, chemical, 242.
stimulus, 230.
stipules, 6, 8.
stomata, 63, 64, 162.
  opening and closing of, 164.
strength of flour, 223.
style, 196.
suberin, 132, 244.
sucrose, 83, 95.
sugars, 83, 97.
sulphate of ammonia, 21, 51.
sulphur bacteria, 149.
Sundew, 19, 154.
surface tension, 114.
suspensoids, 106.
swarm spores, 191.
Sweet pea, 218.
Sycamore, 8.
symbiosis, 54, 152.
synergidae, 200.
Syringa vulgaris, 8.

T

tap-root, 35, 56.
tendrils, 247, 249.
Thallophyta, 22, 23.
thallus, 14.
transpiration, 172.
  amount of, 177, 181.
  current, 184.
Triticum sativum, 32.
turgidity, 104.
turnip-rooted cabbage, 245.

U

Ulex europaeus, 180.

V

Van Helmont, 45.
variation, 189.
variegation, 51, 74.
vascular bundles, 121.
  formation of, 127.
  mode of increase of, 122.
vascular system, 117.
vegetative propagation, 192, 207.
veins, 58.
Venus' fly-trap, 154, 250.
Viburnum Lantana, 6.

Viscum album, 154.
vital proteins, 87.
vitamines, 4.

W

water-culture, 48.
water, excretion of, 168.
Wayfaring tree, 6.
Wheat, 29, 31.
wheat crop, 41.
wind pollination, 197.
woodlands, 17.
wood-vessels, 126.
woody fibres, 127.
wound-hormones, 246.
wounds (healing of), 125, 244.

X

Xanthophyll, 75.
xerophytic plants, 181.

Y

yeast, 24, 143, 147.
Yellow bird-nest, 152.

Z

Zostera maritima, 19.
zygote, 192, 200.
zymase, 144.
zymin, 144.

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